THE ESTABLISHMENT OF THE NEW GENUS *ALTOPARADISIUM* AND A REEVALUATION OF *ARTHROPOGON* (POACEAE, PANICEAE)[1]

Tarciso S. Filgueiras,[2] *Gerrit Davidse,*[3] *Fernando O. Zuloaga,*[4] *and Osvaldo Morrone*[4]

ABSTRACT

Altoparadisium is described as a new genus of Paniceae based on *A. chapadense*, sp. nov., from the campo rupestre habitats of Goiás, Brazil. *Altoparadisium chapadense* is illustrated and fully described morphologically and anatomically. It is extremely unusual in the Paniceae in possessing only two spikelet bracts and in having spikelet reduction from the apex as well as the base. The bracts are interpreted to be homologous to an upper glume and lower lemma. The only flower is interpreted to be homologous to the upper flower of a typical panicoid spikelet. It is a C_4 grass with Kranz anatomy, distinctive Kranz cells, and typical panicoid bicellular microhairs. In order to establish the phylogenetic relationships of *Altoparadisium*, it was included in a cladistic analysis of *Arthropogon* and related genera. We conclude that: (1) *Arthropogon* as traditionally circumscribed is polyphyletic; (2) *Arthropogon scaber* is the sister species of *Altoparadisium chapadense*; it is therefore transferred to this genus as *Altoparadisium scabrum* and illustrated for the first time; (3) *Arthropogon bolivianus* and *A. rupestris* are reduced to varieties of *Altoparadisium chapadense*; (4) *Arthropogon piptostachyus* is recognized as originally described, i.e., as the monotypic genus *Achlaena*; (5) *Arthropogon lanceolatus* should probably be included in a new, monotypic genus, but because its phylogenetic relationships remain unresolved, such a new name is not yet proposed. The recircumscribed genera *Arthropogon* and *Achlaena* are briefly summarized, and a key to their species and varieties is provided.

Key words: Achlaena, Altoparadisium, anatomy, Arthropogon, Arthropogoninae, Brazil, Paniceae, Poaceae, phylogeny, taxonomy.

Chapada dos Veadeiros is one of the 25 physiographic units reported for Brazil by Cochrane et al. (1985). It is located between 13–15°S and 47–49°W, and the altitude varies from 800 to 1700 m. The vegetation is made up principally of campo rupestre but also gallery forests, cerrado (sensu stricto), campo limpo of cerrado, and permanent marshes. The flora of Chapada dos Veadeiros is poorly known. A botanical survey undertaken by Munhoz and Proença (1998) found 106 families, 372 genera, and 751 species, 66 of which were considered endemic. One notable recent discovery from the Chapada dos Veadeiros is a new species of *Triraphis* R. Br. (Poaceae), *T. devia* Filg. & Zuloaga, which documents a New World occurrence for a genus previously thought to be disjunct between Africa and Australia (Filgueiras & Zuloaga, 1999).

During a field excursion to the Chapada dos Veadeiros in September 1994 as part of the project "Biogeography of the Cerrado Biome" (Felfili et al., 1994, 1997), a morphologically unusual grass was collected that seemed to be an undescribed species and could not immediately be assigned to any described genus in the Poaceae (Clayton & Renvoize, 1986; Nicora & Rúgolo de Agrasar, 1987; Webster et al., 1989; Watson & Dallwitz, 1992).

As detailed below, with further studies we indeed determined that this grass represented an undescribed genus, and it is here described and named as *Altoparadisium chapadense*. In order to finalize this conclusion, we also had to consider the relationship of *Altoparadisium* with genera traditionally

included in subtribe Arthropogoninae (Clayton & Renvoize, 1986: 300). This additionally led us to test the monophyly of *Arthropogon*, to investigate the sister-group relationships of *Arthropogon*, and to revise the taxonomy of the species traditionally included in *Arthropogon*.

MATERIALS AND METHODS

The morphological and anatomical studies were based on herbarium specimens from IBGE, MO, SI, and US and supplemented with observation from living specimens cultivated at IBGE. In the taxonomic treatment, we only cite additional voucher specimens not already studied and listed previously by Filgueiras (1982, 1986, 1996).

The standardized terminology for comparative leaf anatomy proposed by Ellis (1976, 1979) was used. Cross-sectional leaf anatomy was determined from hand-sectioned cross sections of leaf blades of herbarium specimens previously treated with ethylene glycol for 24–48 hours. The blades were sectioned approximately one-third from the base, mounted on permanent slides, and then stained using standard anatomical techniques. Some sections were studied without clearing, in order to determine the relative position of the chloroplasts in the Kranz sheaths. The rest were cleared and stained with Alsatian Blue-safranin (Cutler, 1978) or safranin-fast green.

Epidermal preparations for light microscope studies were made following the methodology of Metcalfe (1960). The SEM epidermal studies were done using a Zeiss 940A scanning electron microscope at the Instituto de Botánica Darwinion, Buenos Aires, Argentina.

For the cladistic analysis we used 28 morphological characters and 6 anatomical characters (Appendix 1, Table 1). Two of these (14, 26) are multistate characters and were treated as non-additive (unordered). Most of the data (90%) were obtained directly from herbarium specimens and supplemented with published data. Table 2 contains the data matrix, which was analyzed using Hennig86 version 1.5 (Farris, 1988), applying the option of implicit enumeration, i.e., all polymorphic entries were replaced in the data matrix (Table 2) as missing entries. In parallel, the data matrix was analyzed under parsimony with equal weighting using Nona, version 1.8 (Goloboff, 1993). This analysis was conducted using the default setting *amb*- (clades resolved only if they have unambiguous support) and *poly* = (polytomies allowed), and also utilizing the command mswap*13. Consistency indexes (CI, Kluge & Farris, 1969), and retention

Table 1. List of the characters and character states used in the cladistic analysis.

1. Inflorescence: open (0) closed (1)
2. Pilose callus: absent (0) present (1)
3. Spikelet compression: dorsal (0) lateral (1)
4. Internode between glume 1 and glume 2: absent (0) present (1)
5. Lower glume: absent (0) present (1)
6. Upper glume apex: muticous (0) mucronate or awned (1)
7. Upper glume apex: entire (0) bilobed (1)
8. Lower lemma apex: muticous (0) awned (1)
9. Lower lemma apex: entire (0) bilobed (1)
10. Lower palea: absent (0) present (1)
11. Lower flower: absent (0) present (1)
12. Upper floret compression: dorsal (0) lateral (1)
13. Upper lemma: absent (0) present (1)
14. Upper palea, relative length in relation to the upper lemma: 1/1 (0) 1/4–3/4 (1) 1/4 (2) absent (3)
15. Upper lemma texture: cartilaginous (0) hyaline (1)
16. Lodicules of the upper floret: absent (0) present (1)
17. Functional stamens: three (0) two (1)
18. Parenchyma sheath: absent (0) present (1)
19. Mestome sheath: non-Kranz (0) Kranz (1)
20. Distinctive Kranz cells: absent (0) present (1)
21. Fusoid cells: absent (0) present (1)
22. Intercostal grooves of the upper glume: absent (0) present (1)
23. Vascular bundles below the bulliform cells: absent (0) present (1)
24. Leaf blades: flat (0) cylindrical (1)
25. Hilum type: punctate (0) linear (1)
26. Upper floret color: straw-colored (0) castaneous (1) translucent (2)
27. Germination lid: absent (0) present (1)
28. Upper glume texture: coriaceous (0) herbaceous (1)
29. Lower lemma texture: coriaceous (0) herbaceous (1)
30. Vascular bundles: ordered (0) unordered (1)
31. Awn of the upper glume: straight (0) twisted (1)
32. Spikelet hairs: eglandular (0) glandular (1)
33. Spikelet base: not toroid (0) toroid (1)
34. Lower glume: without rigid tuberculate hairs (0) with tuberculate hairs (1)

indexes (RI, Farris, 1989), were calculated only for informative characters. Bremer support, the number of extra steps needed to lose a branch in the strict consensus of near-most-parsimonious trees (Bremer, 1994), was calculated in order to evaluate the relative support of clades. Similarly, bootstrap analysis was also performed (Felsenstein, 1985). The calculation of branch support values and bootstrap analysis was done with Nona (Goloboff, 1993).

For the construction of the consensus tree, we used the Nelson option of the cited programs. CLADOS (Nixon, 1993) was used for the analysis of the

Table 2. Data matrix used in the cladistic analysis of *Altoparadisium* and related genera. Square brackets "[]" indicate polymorphism in binary characters. For a taxon a hyphen (-) indicates character inapplicable and a question mark (?) indicates character unobserved.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Thyridolepis	1	1	0	0	1	0	0	0	0	[01]	[01]	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	-	0	0	1
Homolepis	0	0	0	0	1	0	0	0	0	1	[01]	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	1	1	1	0	1	0	0	0
Streptostachys	0	0	0	0	1	0	0	0	0	[01]	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	-	0	1	0
Digitaria	0	0	0	0	1	0	0	0	0	[01]	[01]	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	-	0	0	0
Homopholis	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	-	0	0	0
Melinis	0	0	1	0	1	1	1	1	1	[01]	[01]	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	-	0	0	0
Leptocoryphium	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	1	1	1	1	1	-	0	0	0
Anthaenantia	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	0	-	0	0	0
Reynaudia	1	0	1	0	1	1	1	1	1	0	0	1	1	3	3	1	1	0	1	1	0	0	0	0	1	2	0	0	0	0	-	0	0	0
Achlaena	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Altoparadisium chapadense	1	1	0	0	0	1	0	0	0	0	0	0	0	3	-	1	0	1	1	1	0	1	0	0	0	-	1	1	1	0	1	0	0	0
Altoparadisium scabrum	1	1	0	0	1	1	0	0	0	[01]	0	0	1	2	2	1	0	1	1	1	0	1	0	0	0	2	0	1	1	0	0	0	0	0
Arthropogon villosus	0	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	0	1	1	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0
Arthropogon filifolius	0	1	1	0	1	1	1	0	0	1	1	1	1	1	1	0	0	1	1	0	0	0	-	1	?	2	0	0	0	0	0	0	0	0
Arthropogon xerachne	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0	0	?	2	0	0	0	0	0	0	0	0
Arthropogon lanceolatus	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	1	0	0	0	0	?	0	1	1	0	0	0	0	0	0

distribution of the characters in the cladograms and the generation of the different trees.

The taxa included in this analysis are listed in Appendix 2. For the outgroup selection we followed the work of Zuloaga et al. (2000), who analyzed the tribe Paniceae on the basis of morphological and anatomical characters. In this study, Zuloaga et al. (2000) treated *Arthropogon* as three monophyletic subunits. The results indicated that these three subunits were each related to different and distinct taxa of Paniceae, although this analysis could not completely resolve all generic relationships. Consequently, the following taxa were selected as outgroups for *Arthropogon* sensu lato: *Anthaenantia* P. Beauv., *Digitaria* Haller, *Homolepis* Chase, *Leptocoryphium* Nees, *Melinis* P. Beauv., *Reynaudia* Kunth, *Streptostachys* Desv., *Homopholis* C. E. Hubb., and *Thyridolepis* S. T. Blake. Among these genera, the tree was rooted in *Thyridolepis* on the basis of possessing the C_3 photosynthetic pathway, which has been suggested to be ancestral to the C_4 pathway (Brown, 1977; Kellogg & Campbell, 1987). Also, Clayton and Renvoize (1986: 267) placed the subtribe Neurachninae (S. T. Blake) Clayton & Renvoize (= Neurachneae S. T. Blake, Watson & Dallwitz, 1992) at the base of the tribe Paniceae and proposed that the inclusion of taxa with non-Kranz anatomy, with the upper lemma not specialized, and the presence of 3 stigmas suggests an early split from the mainstream Paniceae. Similarly, Kellogg and Watson (1993) rooted the trees for their study of the Andropogodae L. Liou at *Thyridolepis*; and recently Wills et al. (2000), in their revision of *Homopholis*, also rooted the trees in the Neurachneae and *Thyridolepis*.

SPIKELET MORPHOLOGY AND LEAF ANATOMY OF *ALTOPARADISIUM CHAPADENSE*

The subfamilial and tribal affinities of the majority of grass species can usually be very readily deduced from spikelet and inflorescence morphology alone. However, that was not the case with *Altoparadisium chapadense*. Its spikelets consist of only two bracts (Fig. 1C–F). On the one hand, its very simple spikelet makes it distinctive, but on the other hand, this very simplicity makes an interpretation of the homology of the spikelet bracts difficult. For this reason we relied primarily on anatomical evidence to deduce its tribal affinities. From this basic anatomical deduction, we then considered a number of hypotheses of spikelet interpretation based on trends in spikelet morphology of putative relatives, especially *Arthropogon*.

Altoparadisium chapadense has a C_4 anatomical organization. This is most clearly evidenced from the presence of only 2 or 3 chlorenchyma cells between all adjacent vascular bundles, a character that is most highly correlated with grass species that have C_4 photosynthesis (Hattersley & Watson, 1975). In addition, since no cells intervene between the metaxylem vessel elements and the laterally adjacent chlorenchymatous, bundle sheath (Kranz) cells in the primary lateral vascular(XyMS-), this indicates that it probably is an NADP-ME type genus (Hattersley & Watson, 1975, 1976).

Additional confirmation of the C_4 status of *A. chapadense* was provided through an analysis of ^{12}C and ^{13}C ratios. It has been firmly established that $\delta^{13}C$ values of -9 to -16% indicate C_4 photosynthesis, while $\delta^{13}C$ values of -23 to -32% indicate C_3 photosynthesis (Smith & Brown, 1973). A leaf sample of a potted plant of *A. chapadense* was analyzed by H. Ziegler (Institut für Botanik und Mikrobiologie, Technische Universität, München, Germany) for its $\delta^{13}C$ value, with the following result: -11.82 (Ziegler, pers. comm.). Thus, according to well-established criteria, the value obtained in this analysis is an independent confirmation that *A. chapadense* is a C_4 species.

The cross-sectional leaf anatomy of *Altoparadisium* is especially distinctive due to the occurrence of isolated bundle sheath cells, known as distinctive Kranz cells (Sánchez & Arriaga, 1989; Sánchez et al., 1989), in the mesophyll between adjacent vascular bundles (Fig. 2B). These cells have also been called distinctive cells (Tateoka, 1958), circular cells (Metcalfe, 1960), axillary bundle cells (Renvoize, 1982a, b), and specialized parenchyma cells (Reger & Yates, 1979). As noted by Renvoize (1982a), these distinctive Kranz cells are similar in structure and function to bundle sheath cells, and are the equivalent to a vascular bundle and bundle sheath reduced to a single cell (Tateoka, 1958). The number of chlorenchymatous mesophyll cells between adjacent vascular bundles and adjacent distinctive Kranz cells or between adjacent distinctive Kranz cells is two or three. This is a strong indication that *Altoparadisium* is a C_4 genus (Hattersley & Watson, 1975). Distinctive Kranz cells have so far only been reported in subfamily Panicoideae in five genera of the tribe Arundinelleae and four genera of Paniceae (reviewed in Morrone et al., 1995, who list one additional genus, *Achlaena*, a genus included in *Arthropogon* by Filgueiras, 1982). This is good evidence that *Altoparadisium* belongs in the Panicoideae.

Finally, the occurrence of microhairs of the two-celled, thin-walled type with a tapering distal cell, usually called the panicoid type, is additional,
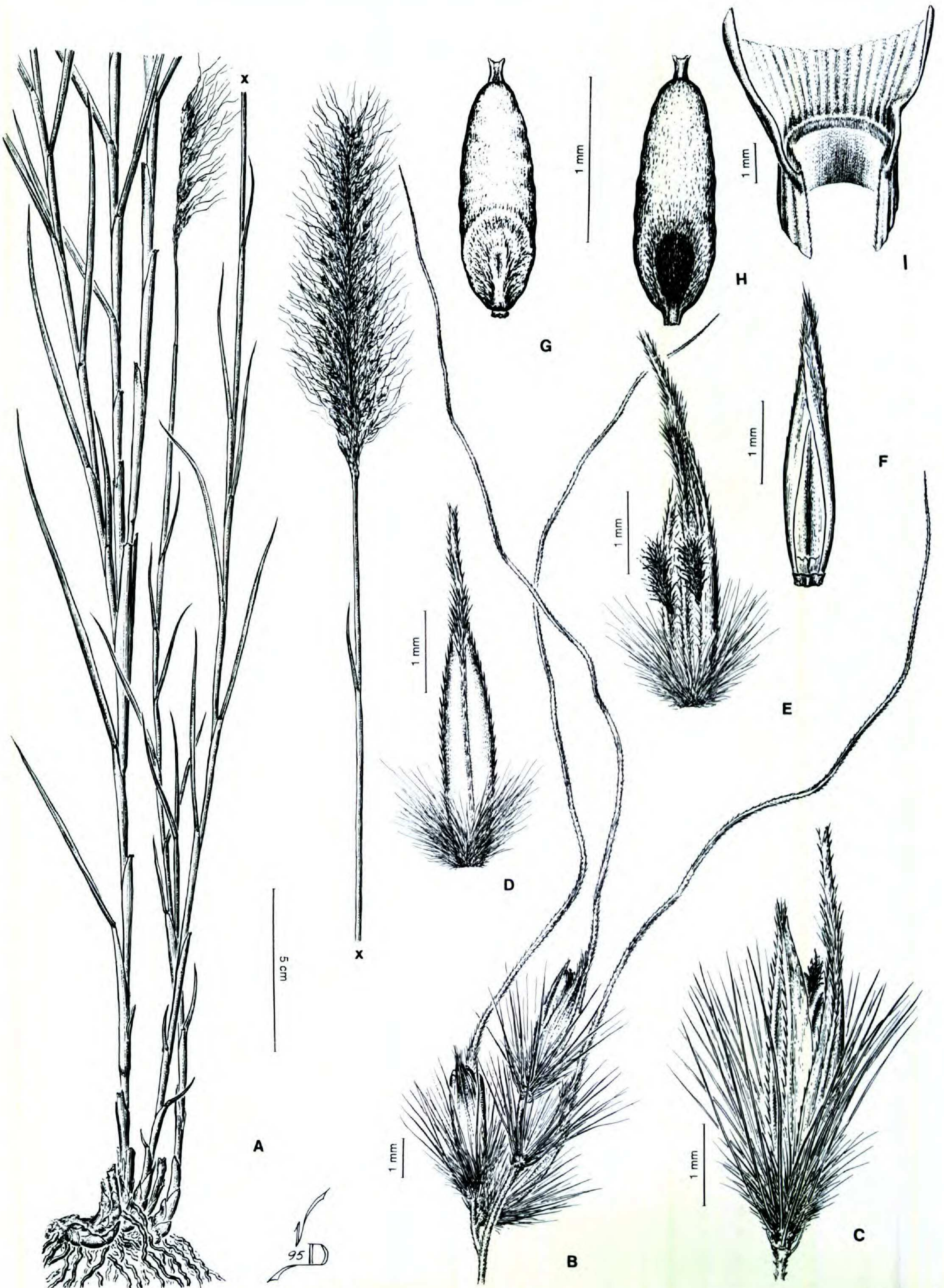
Figure 1. *Altoparadisium chapadense* (based on *Filgueiras & Fonseca 2987*). —A. Habit. —B. One spikelet pair and two solitary spikelets on the ultimate portion of an inflorescence branch; note prominent awn of the upper glumes (awn of lowest spikelet not drawn). —C. Attached spikelet seen from the lower lemma side with prominent hairs at the apex of the pedicel and the base of the callus. —D. Lower glume, 3-nerved. —E. Detached spikelet seen from the lower lemma side with prominent callus hairs and laterally exserted stigmas. —F. Lower lemma, ventral view, with 2 lodicules at the base. —G. Caryopsis, embryo side. —H. Caryopsis, hilum side. —I. Ligule. All drawings by Vladimiro Dudás.
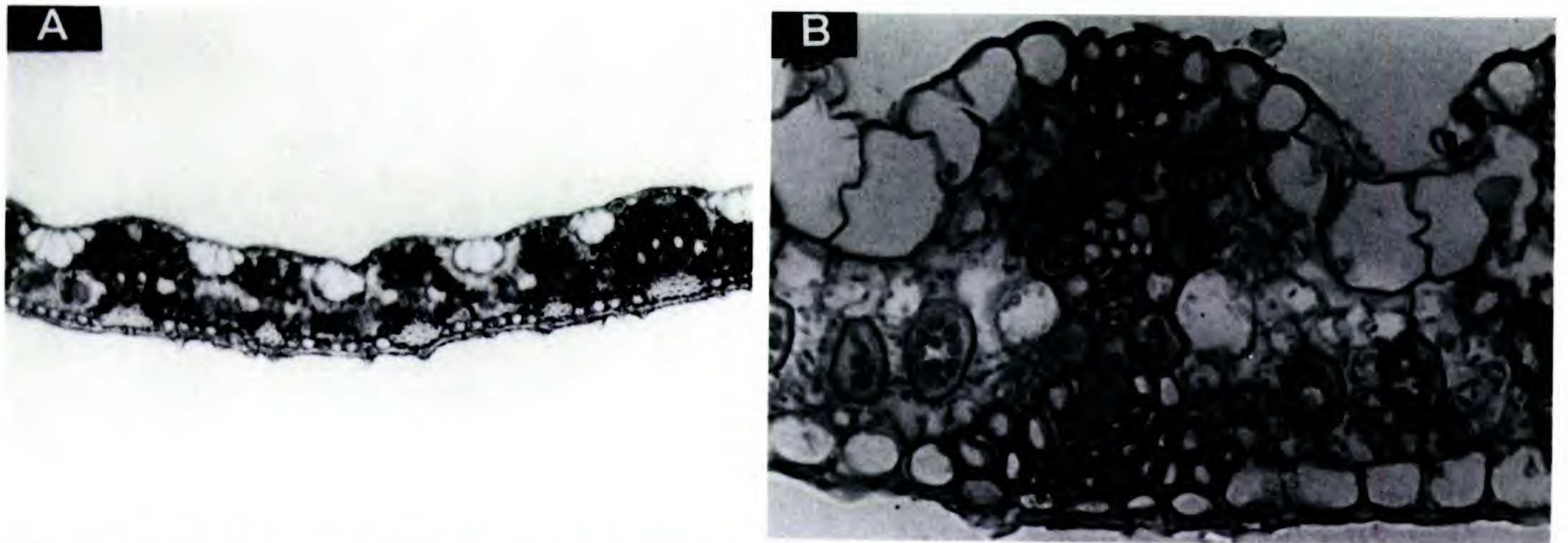
Figure 2.   Leaf anatomy of *Altoparadisium chapadense*, cross-sectional leaf anatomy (based on *Filgueiras & Fonseca 2987*). —A. Cross section of a portion of the leaf blade, showing the midrib with a single first-order vascular bundle, three third-order vascular bundles, and one first-order lateral bundle. —B. Cross section of a third-order vascular bundle; note the prominent outer parenchyma sheath and the three distinctive Kranz cells on each side of the bundle.

strong evidence that *Altoparadisium* belongs in the Panicoideae (Fig. 3C, D) (Watson & Dallwitz, 1992).

Only one previously described panicoid grass has spikelets consisting of only two bracts and a single flower, *Paspalum soukupii* Carbonó, a species of the *Racemosa* group (Morrone et al., 1995). However, in *P. soukupii* the inflorescence consists of unilateral, winged racemes, totally different from the verticillate panicle of *Altoparadisium*. Furthermore, the spikelets of *Paspalum soukupii* unambiguously represent an upper floret with the typical palea and lemma of species of the group *Racemosa* or, indeed, any species of *Paspalum*. And, although distinctive Kranz cells do occur in *P. soukupii*, as well as all other nine species of *Paspalum* group *Racemosa* (Morrone et al., 1995: 112), spikelet and inflorescence morphology conclusively eliminate this group of species from further consideration as a possible close relative.

From these considerations we concluded that *Altoparadisium* represented an undescribed genus, and we continued our search for putatively related genera among the other eight genera with distinctive Kranz cells (Morrone et al., 1995). Spikelet structure is quite different in all genera of Arundinelleae, and we did not consider this tribe further. Similarly, *Anthephora* Schreb., *Dissochondrus* (Hillebr.) Kuntze, and *Paspalum* L., three of the genera of Paniceae R. Br. with distinctive Kranz cells also seem quite different in specialized spikelet and inflorescence morphology and are, therefore, probably not good candidates as possible relatives. However, in inflorescence architecture, spikelet shape and size, ligule type (a minute ring of hairs), and the ring of callus hairs at the base of the spikelet, *Altoparadisium* resembles some spe-

cies of *Arthropogon*. Specifically, the inflorescence of *Altoparadisium* resembles that of *Arthropogon scaber*, *A. bolivianus*, and *A. rupestris* (Filgueiras, 1982, 1986, 1996) in being a contracted terminal panicle with a tough rachis, pilose nodes, and verticillate branches, but it differs in being pointed at the apex, and in its whitish not greenish or stramineous color. *Altoparadisium* further differs from *Arthropogon* species by the presence of a ring of hairs at the apex of the pedicel, its soft spikelet texture (membranous, not coriaceous), and the possession of only two spikelet bracts, instead of four, five, or six.

Because of the resemblance in the anatomy and inflorescence structure, and because both genera occur in the same geographical region, we hypothesized that *Arthropogon* may be the closest extant relative of *Altoparadisium*. The interpretation of spikelet structure in *Altoparadisium* was, therefore, primarily made with reference to variation patterns in *Arthropogon* and secondarily to the closely related *Reynaudia* Kunth, a monotypic Cuban genus. For the purpose of this discussion, we follow the classification of Clayton and Renvoize (1986), who place *Arthropogon* and *Reynaudia* in the subtribe Arthropogoninae Butzin of the tribe Paniceae. The recognition of the subtribe is based primarily on the more strongly indurate texture of the glumes and lower lemma compared to that of the upper floret, as well as the laterally compressed and solitary spikelets. *Arthropogon* and *Reynaudia* spikelets typically have two glumes and two florets. Although the spikelets are usually said to be laterally compressed (Filgueiras, 1982, 1986; Clayton & Renvoize, 1986; Watson & Dallwitz, 1992), *Arthropogon* as traditionally circumscribed is actually heterogeneous in this regard (Zuloaga et al., 2000),
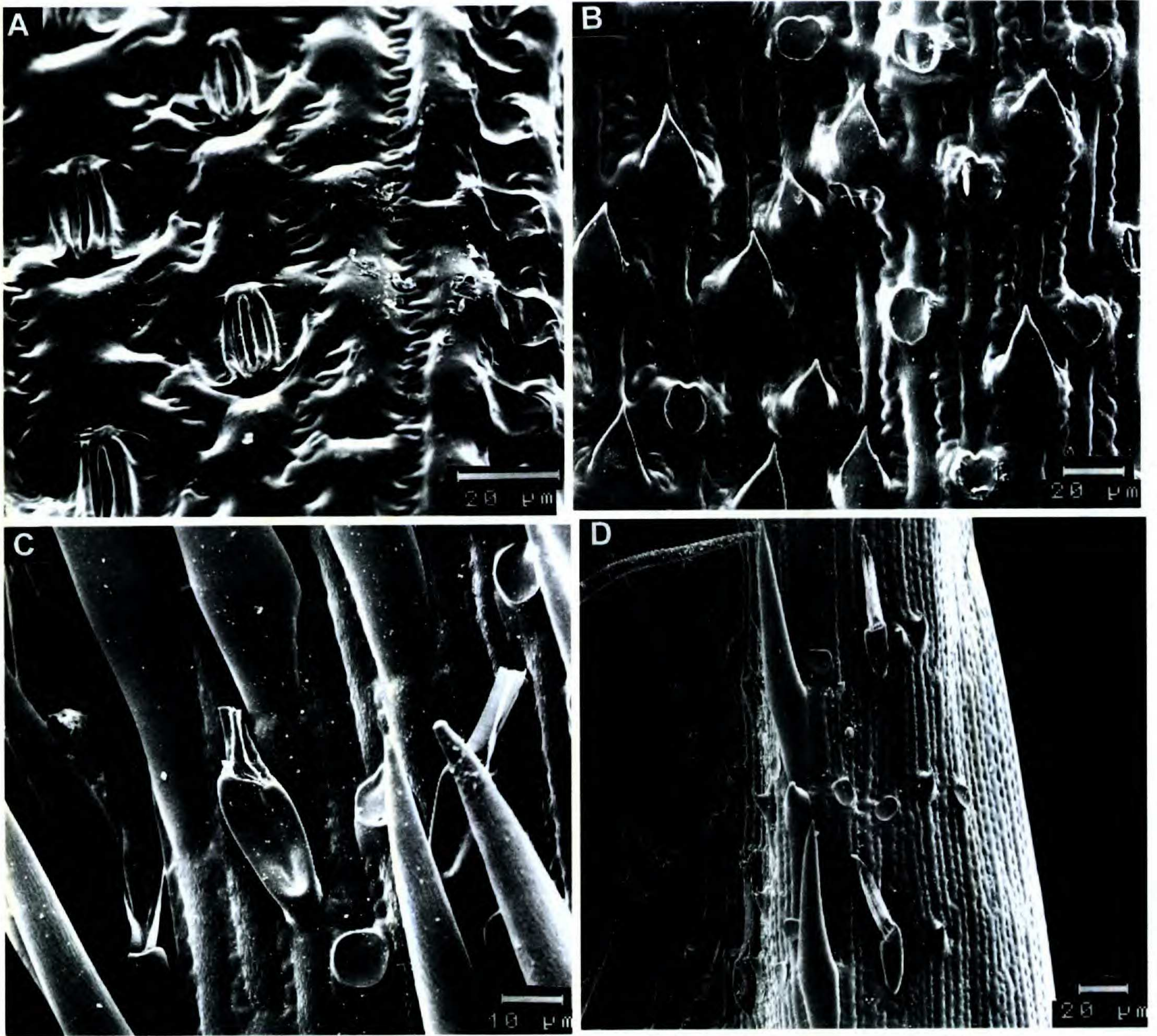
Figure 3.   SEM photographs of leaf, palea, and lemma epidermal anatomy of *Altoparadisium chapadense*, in surface view (based on *Filgueiras & Fonseca 2987*). —A. Abaxial surface of the leaf blade with stomata and long cells in the intercostal zone, and silica bodies and long cells in the costal zone. —B. Adaxial surface of the leaf blade with silica bodies, prickles, and long cells. —C. Detail of the apex of the upper glume with macrohairs, bicellular panicoid microhairs, prickles, and a few silica bodies. —D. Detail of the apex of the lower lemma with numerous macrohairs, bicellular panicoid microhairs with the apical cells collapsed, and silica bodies.

as well as in several other important diagnostic characters, such as presence of a pilose callus, texture of the upper floret, hilum type, and anatomical characters. In *A. scaber*, *A. rupestris*, and *A. bolivianus* the spikelets are clearly dorsally compressed.

The following patterns of variation in spikelet parts are known in *Arthropogon* and *Reynaudia*. Bract number in *Arthropogon* species is six, five, or four and in *Reynaudia* four. In both genera the glumes are coriaceous or firmly membranous and awned. The lower glume varies from an awned, broad-based membrane to just an awn; the upper glume always has a fully developed membrane and is awned. The lower floret is always present. The lower flower is staminate or absent. The lower lem-

ma generally has the same texture as the upper glume but bears no or only a small awn. The lower palea varies from 4/5 as long as the lemma to absent, and when present, is hyaline. The upper floret is always present and always has a bisexual flower. The upper lemma is always present but is reduced in size compared to the lower lemma. The upper lemma is membranous or, more commonly, hyaline in texture and may totally lack nerves. The upper palea varies from as long as the upper lemma, to half as long or entirely absent. When present it is hyaline, and when well developed, it has a typical 2-keeled, 2-nerved morphology as present in most grass genera.

We used the following criteria in our interpre-

tation of *Altoparadisium* spikelet morphology and bract homology.

(1) Since neither of the bracts is 2-keeled, it is unlikely that either represents a palea, although there are a significant number of exceptions to two-keeled paleas in the family. For example, in the DELTA Grass Genera of the World database, Watson and Dallwitz (1992 onward) list 63 genera as having at least some species with nerveless paleas, 23 genera with 1-nerved paleas, 71 genera with multinerved paleas, and 579 genera with 2-nerved paleas.

(2) Since both lower and upper paleas are variably developed in *Arthropogon* and entirely absent in *Reynaudia*, this suggests the possibility that they may have been lost entirely in *Altoparadisium*.

(3) Since the lower flower is quite variable in its development in the Panicoideae, including *Arthropogon* species, where they vary from male flowers to completely absent, and totally absent in *Reynaudia*, we hypothesize that the lower flower is also entirely absent in *Altoparadisium*. This then means that the solitary flower of *Altoparadisium* is homologous to the upper flower typically present in panicoids.

(4) Since the lower glume of *Arthropogon* is variably developed, this may indicate that it disappeared in *Altoparadisium*.

(5) Since the upper lemma is more variable in its development among *Arthropogon* species than the lower lemma, we hypothesize that it has also disappeared in *Altoparadisium*.

(6) In this process of elimination, the remaining bracts would, therefore, be homologous to the upper glume and the lower lemma of the typical panicoid spikelet. As in *Arthropogon* species and in *Reynaudia*, the texture of the upper glume is the same as that of the lower lemma. Oddly enough, these two bracts subtend the only remains of the upper floret, the upper flower.

Early in our study of *Altoparadisium* we considered a number of other interpretations of the homology of the spikelet bracts including the following: the two bracts represent (1) an upper lemma and upper palea, (2) a lower and upper glume, (3) a lower and upper lemma. In the absence of developmental studies, which might provide more definite evidence but which were beyond the scope of this project, the decisive evidence for the interpretation presented above was a side-by-side comparison of the spikelets of *Altoparadisium chapadense* and *Arthropogon scaber*. The overall gestalt of the two spikelets is very similar. If one then imagines the absence of the lower glume and upper lemma (Fig. 7), then in the texture, compression, and con-

firmation of the nerves and internerves, the remaining two bracts of such an *A. scaber* spikelet look very much like the corresponding bracts of the *Altoparadisium* spikelet (Fig. 1).

Summarizing, in Arthropogoninae (sensu Clayton & Renvoize, 1986) we hypothesize a reduction series in spikelet morphology that proceeds primarily from the apex to the base and secondarily from the base to the apex. In contrast to the sequence just postulated, the most common pattern of spikelet reduction in the rest of the Paniceae usually proceeds from the base to the apex and results in a tendency to reduce the lower glume before the upper glume and the lower floret and its component parts before the upper floret and its component parts (see Cialdella & Vega, 1996, and references cited therein).

Once this initial anatomical and morphological analysis had been completed, it then became evident that in order to gain a better understanding of the relationships of *Altoparadisium chapadense*, it would be desirable to do a phylogenetic analysis of any of the putatively related taxa.

DISCUSSION

The cladistic analysis of the data matrix (Table 2) gave three equally parsimonious cladograms, using Hennig86; each cladogram was 57 steps long, with a consistency index of 0.52, and a retention index of 0.72 (Fig. 4). One of these cladograms (Fig. 6) is illustrated, including all character state changes. The strict consensus tree is shown in Figure 5, along with the Bremer support values and bootstrap percentages for each node.

A single equally parsimonious cladogram was obtained from the data matrix using Nona; this cladogram has an identical topology to the one illustrated in the strict consensus tree of Figure 5.

MONOPHYLY OF *ARTHROPOGON*

In order to test the monophyly of *Arthropogon* and search for a sister to *Altoparadisium*, we included the genera *Melinis* (subtribe Melinidinae), *Reynaudia* (Arthropogoninae), *Homopholis, Digitaria, Leptocoryphium,* and *Anthaenantia* (Digitarinae), and *Homolepis* and *Streptostachys* (Setariinae). All taxa were rooted with *Thyridolepis* (Neurachninae).

The analysis showed that *Arthropogon* as traditionally circumscribed is polyphyletic (Fig. 6 shows one of the three trees with all characters). *Arthropogon lanceolatus* is the most basal member of the ingroup and could be circumscribed as a monotypic genus; it forms a monophyletic clade with *Streptostachys + Homolepis*, which is supported by the presence of fusoid cells (character 21). The boot-
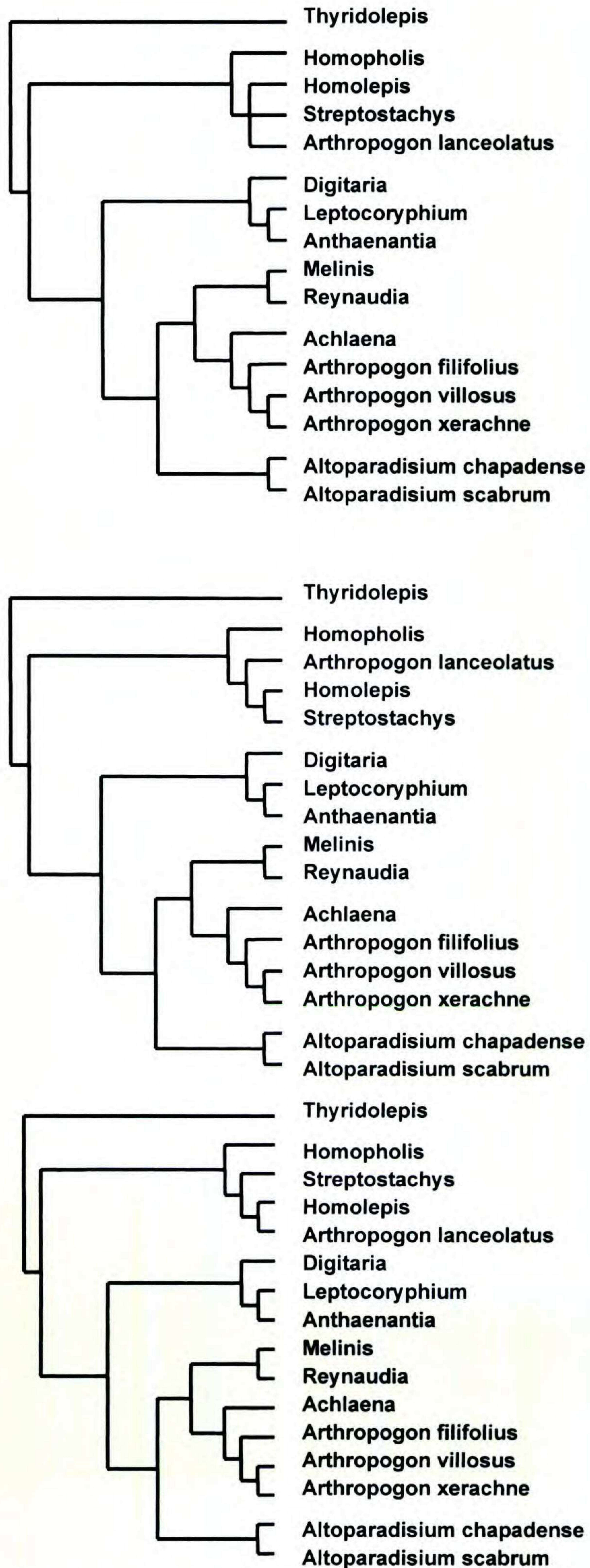
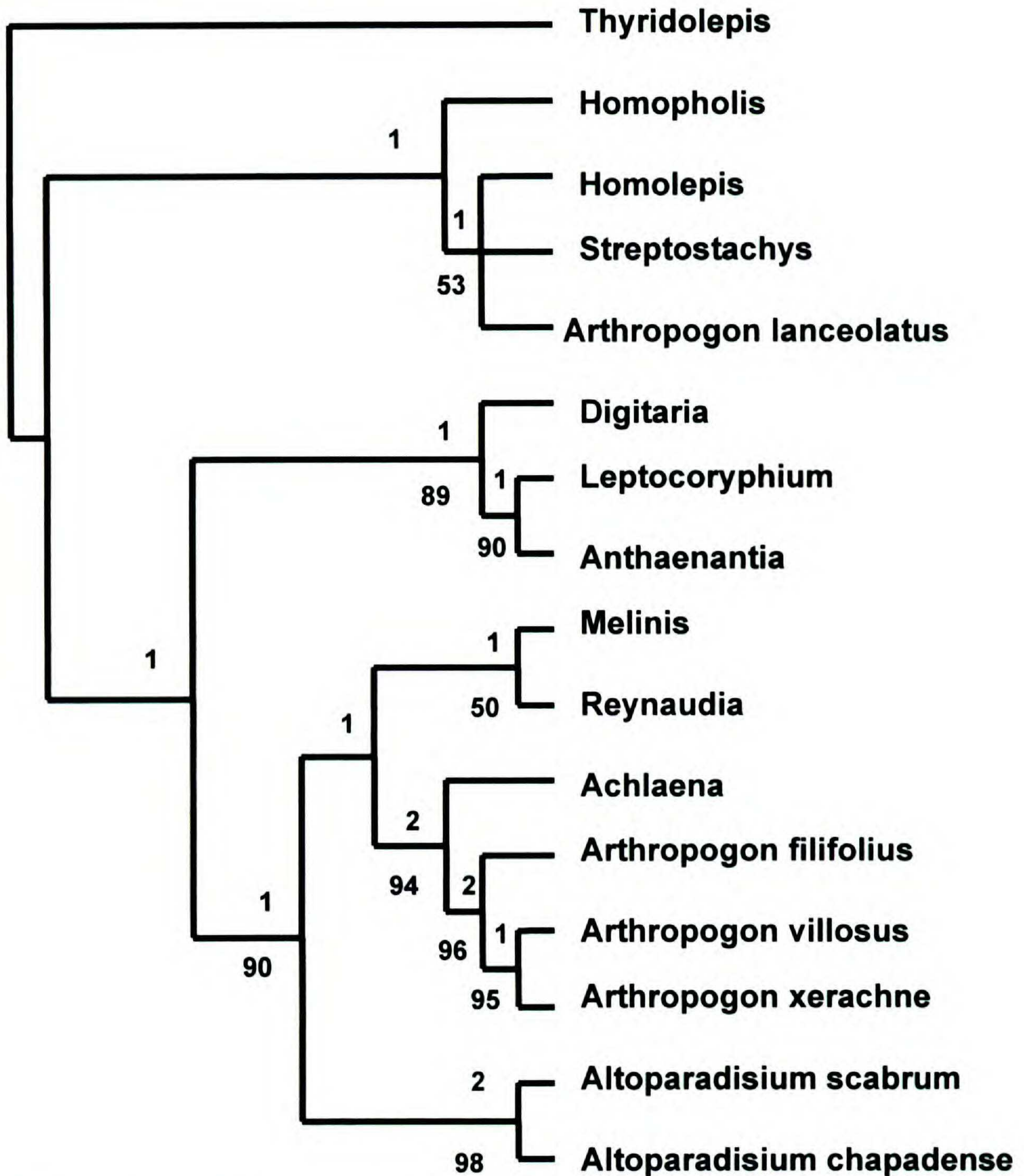Figure 4.   Equally parsimonious trees obtained from the data matrix (Table 2).

Figure 5. Strict consensus tree derived from the three equally most parsimonious trees. The upper numbers on each branch indicate the Bremer support values, while the lower numbers indicate bootstrap percentages.

strap value for this group is low (53). A similar topography was shown in a previous analysis (Zuloaga et al., 2000).

Altoparadisium chapadense and *A. scabrum* form a clade, supported by two synapomorphies: the relative development of the upper palea ¼ or less as long as the upper lemma (character 14), and the presence of intercostal grooves on the upper glume (character 22). This is clear support that these two species are congeneric, and for this reason we transfer *Arthropogon scaber* to *Altoparadisium*. Within this clade, *A. chapadense* is distinguished by the lower glume absent (character 5), upper lemma absent (character 13), upper palea absent (character 14), and awn of the upper glume twisted

(character 31). In the initial scoring of the characters, it became evident that *Arthropogon scaber*, *A. rupestris*, and *A. bolivianus* could not be differentiated using the characters of the cladistic analysis. Consequently, we consider these three taxa to represent a single species. However, these taxa seem at least modally distinct in the degree of leaf blade infolding and scabrosity, as well as spikelet and inflorescence size. For this reason we do recognize them at the varietal level and make the necessary new combinations below.

The *Melinis–Reynaudia* clade, although poorly supported with a bootstrap percentage of only 50, is a sister to the *Achlaena piptostachya–Arthropogon* sensu stricto clade. The latter clade is sup-
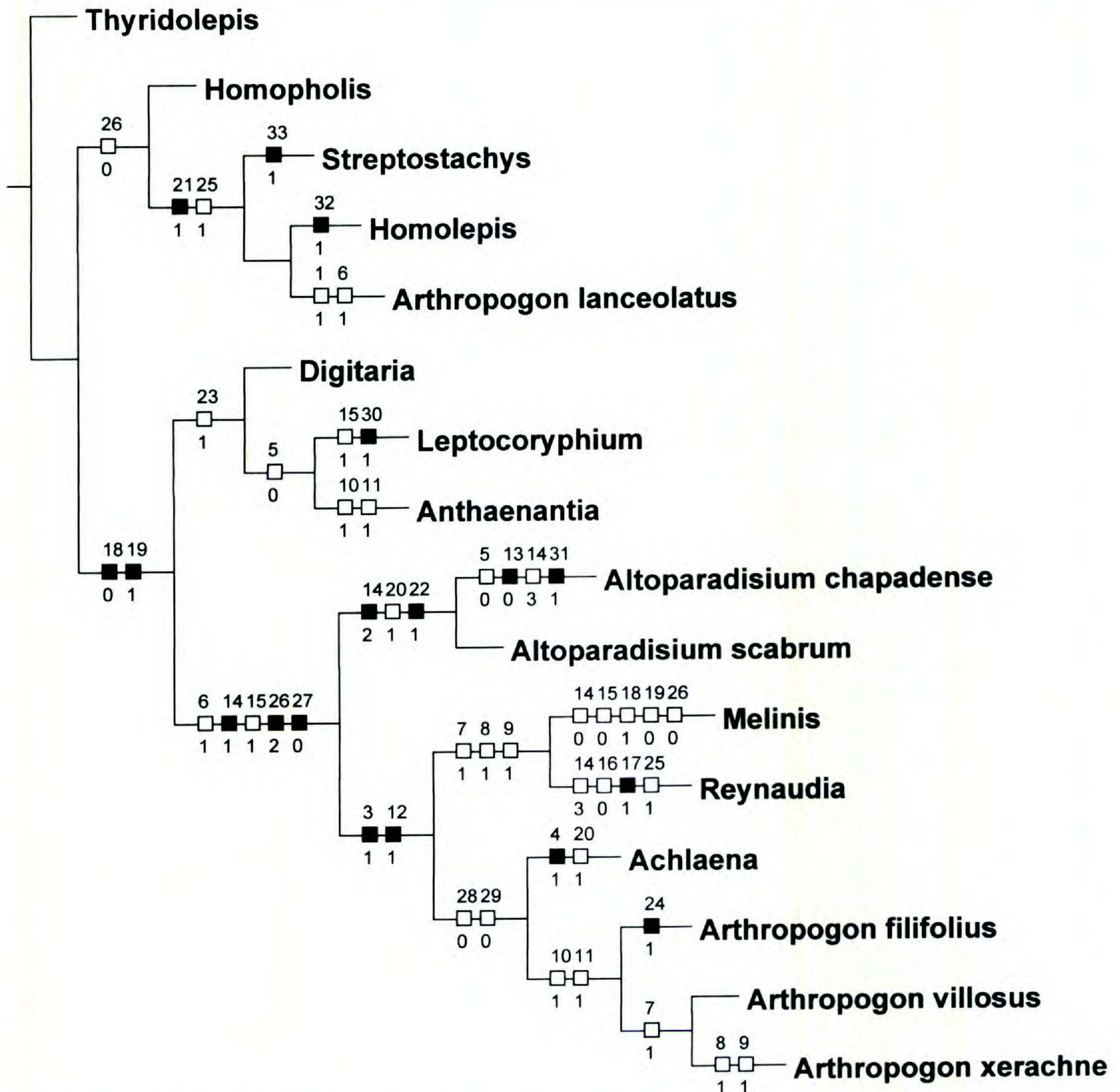
Figure 6. Cladogram of one of the three most parsimonious trees; the character numbers marked with the solid bars indicate synapomorphies, those with hollow bars homoplasious characters. L (length): 57; RI (retention index): 0.72; CI (consistency index): 0.52.

ported by two homoplasious characters, coriaceous upper glume (character 28), and coriaceous lower lemma (character 29), and is strongly supported with a bootstrap percentage of 94. Within this clade, *Arthropogon piptostachyus* is distinguished by two autapomorphies, the presence of a notable internode between the lower and upper glume (character 4), and the presence of distinctive Kranz cells (character 20). The clade formed of *A. filifolius–A. xerachne* is supported by two apomorphies, the presence of a palea (character 10) and lower flower (character 11), and it has strong bootstrap support (94). In addition to its morphological distinctiveness the Cuba-Jamaica endemic, *Achlaena*

piptostachya, is geographically disjunct from the central Brazilian species of *Arthropogon* sensu stricto. These two factors combined give good support for the continued recognition of *Achlaena* as a separate genus.

In summary, as a result of this study we restrict *Arthropogon* to *A. xerachne*, *A. villosus*, and *A. filifolius*; *Arthropogon scaber* is transferred to the new genus *Altoparadisium*; *Arthropogon piptostachyus* is again recognized as *Achlaena piptostachya*; and finally, *Arthropogon lanceolatus* should be excluded from the genus *Arthropogon*, but its exact relationships and position in the tribe Paniceae remain unresolved. This can be explained by inspection of

the character distribution on the cladogram, which indicates there are relatively few nodes that are unambiguously supported by non-homoplasious characters. This is expressed statistically by the low consistency index, as well as by low bootstrap percentiles.

TAXONOMIC TREATMENT

HISTORY OF ARTHROPOGON AND ITS SUPRAGENERIC CLASSIFICATION

The genus Arthropogon has a long and complex history. It was described by Nees (1829) on the basis of one species, A. villosus, from Brazil. Subsequently Hackel (1887) amplified the description of the genus and illustrated A. villosus. Ekman (1911), Pilger and Kuhlmann in Kuhlmann (1922), and more recently Filgueiras (1981, 1982, 1986, 1996) described new taxa in Arthropogon. Filgueiras (1982) revised the genus and has recognized eight species (Filgueiras, 1996).

The position of the genus in the Panicoideae has been controversial. Nees (1829), when describing it, included Arthropogon in the Saccharinae Griseb. Kunth (1833) and Steudel (1853–1855) included the genus in the tribe Andropogoneae Dumort. Bentham and Hooker (1883) and Hackel (1887) placed it in the tribe Tristegineae Benth. & Hook. f. Hitchcock (1936) included the genus in the Melinideae Hitchc., together with Arundinella Raddi and Melinis P. Beauv. Bews (1929) and Roshevits (1937) separated Arundinella, Trichopterix Chiov., Danthoniopsis Stapf, and other genera in the Arundinelleae, and included Melinis and Arthropogon in the Melinidinae. Pilger (1954) for the first time proposed the tribe Arthropogoneae Pilg. ex Butzin, and included Arthropogon, Achlaena Griseb., Reynaudia, and Snowdenia C. E. Hubb. However, his name remained invalid because he did not provide a Latin diagnosis or description. Butzin (1972) later validated the name and reviewed the taxonomy.

Tateoka (1963) indicated that of the four genera included by Pilger in the Arthropogoneae, Snowdenia does not pertain to this group. However, the other three genera are related and share the following characters: upper lemma membranous, glumes somewhat indurate, spikelets with lateral compression, and stigmas with terminal exsertion. Furthermore, based on anatomical characters, Tateoka (1963) suggested that Arthropogon could represent a taxon intermediate between the Arundinelleae and Paniceae.

Filgueiras (1982) illustrated and described the morphological and anatomical variation in Arthropogon. He classified it in the tribe Arthropogoneae, subtribe Arthropogoninae, together with Reynaudia and Snowdenia, following the criteria proposed by Pilger (1954): spikelets solitary; upper lemma thinly membranous, awnless and 1–3-nerved; upper palea thinly membranous, weakly nerved or nerveless.

Clayton and Renvoize (1986) included Arthropogon and Reynaudia in the subtribe Arthropogoninae and included Snowdenia in subtribe Cenchrinae Dumort. They noted the close affinity of Snowdenia with Pennisetum Rich. subsect. Beckeropsis (Fig. & De Not.) Hack. and hypothesized that Snowdenia was probably derived from it by suppression of the bristles subtending the spikelets. Snowdenia possesses dorsally compressed spikelets, a reduced lower glume, and has terminally exserted stigmas. When describing the genus, Hubbard (1929) grouped Snowdenia with Acritochaete Pilg. (subtribe Melinidinae of Clayton & Renvoize, 1986) because they have a similar inflorescence and spikelet morphology.

Grisebach (1866) described the genus Achlaena as monotypic and endemic to Cuba, based on A. piptostachya. Pilger (Hoehne & Pilger, 1922) transferred it to Arthropogon, and this has been generally accepted (Tateoka, 1963; Filgueiras, 1982; Clayton & Renvoize, 1986; Webster et al., 1989). However, Watson and Dallwitz (1992) recognized Achlaena at the generic level based on its restriction to Cuba and the following morphological characters: inflorescence open, spikelets compressed laterally, callus hairy, glumes 2 and narrow, and the upper lemma awnless and acuminate.

Brown (1977), based on anatomical characters, recognized the tribe Arthropogoneae and included Achlaena, Arthropogon, and Reynaudia. He emphasized that the relationship of Snowdenia (African) with the other three genera (American) is questionable because, following Tateoka (1963), Snowdenia has minute and membranous glumes, dorsally compressed spikelets, and stigmas exserted from the tip of the floret.

Webster et al. (1989) basically characterized Arthropogon by the presence of a differentiated callus at the base of the spikelet, spikelets laterally compressed, lower glume awned, and the upper lemma hyaline to membranous.

KEY TO THE GENERA ALTOPARADISIUM, ACHLAENA, AND ARTHROPOGON

1a. Spikelets dorsally compressed; upper palea absent or reduced; intercostal areas of the upper glume prominently sulcate .... Altoparadisium
1b. Spikelets laterally compressed; upper palea well developed; intercostal areas of the upper glume flat.
    2a. Spikelets stipitate; distinctive Kranz cells present .... Achlaena
    2b. Spikelets not stipitate; distinctive Kranz cells absent .... Arthropogon

Altoparadisium Filg., Davidse, Zuloaga & Morrone, gen. nov. TYPE: *Altoparadisium chapadense* Filg., Davidse, Zuloaga & Morrone.

Hoc genus novum *Arthropogoni* Nees simile sed spiculis dorsaliter compressis, palea supera redacta vel nulla, nervis intercostalibus glumae superae manifeste sulcatis absimile.

Plantae perennes, caespitosae. Culmi erecti. Inflorescentia paniculata, contracta, terminalis. Spiculae solitariae vel binatae, anguste oblongo-lanceolatae, dorsaliter compressae; callus non manifestus sed pilis densis, verticillatis ornatus; spiculae 2–4 bracteis munitae; gluma inferna nulla vel setacea; gluma supera spiculam aequans, membranacea, 3–5-nervia, arista irregulariter tortili ornata; palea inferna nulla; flosculus infernus nullus lemmati infero redactus; lemma inferum membranaceum vel herbaceum, 3-nervium, nervus medianus piloso-hispidus, internervi sulcati; palea inferna nulla; flos inferus nullus; lemma superum hyalinum, 3-nervium vel nullum; palea supera redacta, ⅕ lemma aequans, hyalina sive nulla; flos unicus, bisexualis; lodiculae 2, conduplicatae; stamina 3; stigmata 2, purpurea, discreta. Caryopsis anguste oblongo-lanceolata, dorsaliter compressa, basibus stylorum persistentibus; hilum ellipticum ad oblanceolatum, atro-brunneum, ca. ⅕ caryopsidem aequans; embryo ca. ⅓ caryopsidem aequans.

Caespitose perennials. Culms erect; internodes hollow. Leaves primarily cauline; sheaths round on the back, the margins free; auricles absent; ligule a minute fringe of hairs; collar undifferentiated; blades linear-lanceolate. Inflorescence a contracted, terminal panicle; rachis glabrous, tough; nodes pilose; branches verticillate. Axillary inflorescences absent. Pedicels of unequal length. Spikelets paired or solitary, all alike, dorsally compressed, narrowly oblong-lanceolate in outline, disarticulating below the bracts and falling as a unit, with only one bisexual flower; callus undifferentiated except for a dense whorl of colorless hairs at the base of the spikelet; spikelet bracts 2 to 4; lower glume absent to setaceous; upper glume as long as the spikelet, embracing the lower lemma almost entirely, membranous, 3- to 5-nerved, the lateral nerves pilose-hispid or scabrous, the midnerve pilose-hispid toward the apex, projected into a straight or irregularly twisted awn; lower floret reduced to only a lemma; lower lemma membranous or herbaceous, 3-nerved, the midnerve prominent, pilose-hispid, the internerves sulcate, the margins hyaline and sharply folded at the lateral nerves, the apex pointed; lower palea absent; lower flower absent; upper lemma hyaline, 3-nerved, or absent; upper palea reduced, up to ⅕ as long as the upper lemma, hyaline, or absent; flower bisexual; lodicules 2, conduplicate; stamens 3; ovary glabrous; stigmas 2, separate, purple. Caryopsis narrowly oblong-lanceolate in outline, dorsally compressed, light brown, with persistent stylar bases, loosely fitting inside the glumes when fully developed; hilum elliptical to oblanceolate, dark brown, ca. ⅕ as long as the caryopsis; embryo about ⅓ as long as the caryopsis.

KEY TO THE SPECIES AND VARIETIES OF *ALTOPARADISIUM*

1a. Lower glume and upper lemma absent; upper palea absent; upper glume with a twisted awn ⸺
⸺⸺⸺⸺⸺⸺⸺⸺⸺⸺ *A. chapadense*
1b. Lower glume and lemma present; upper palea present; upper glume with a straight awn.
2a. Leaf blades tightly involute ⸺⸺
⸺⸺⸺⸺⸺⸺ *A. scabrum* var. *bolivianum*
2b. Leaf blades flat.
3a. Spikelets 6–7 mm long; leaf blades scabrous; inflorescences 15–25 cm long ⸺
⸺⸺⸺⸺⸺ *A. scabrum* var. *scabrum*
3b. Spikelets 4–5 mm long; leaf blades smooth; inflorescences 7–9 cm long ⸺
⸺⸺⸺⸺⸺ *A. scabrum* var. *rupestre*

1. Altoparadisium chapadense Filg., Davidse, Zuloaga & Morrone, sp. nov. TYPE: Brazil. Goiás: Chapada dos Veadeiros, município of Alto Paraíso, ca. 26 km a oeste of Alto Paraíso, ca. 14°07′S–47°30′W, campo rupestre, estrada para Colinas do Sul Goiás, 5 Sep. 1994, *T. S. Filgueiras & M. L. Fonseca 2987* (holotype, IBGE!; isotypes, ICN!, K!, MO!, SI!, SP!, US!). Figure 1.

Altoparadisio scabro (Pilg. & Kuhlm.) Filg. et al. simile sed spiculis duabus tantum bracteis et aristis tortilibus differt.

Moderately caespitose, rhizomatous perennials. Rhizomes small, knotty, superficial; young rhizomes covered with cataphylls. Culms 75–80 cm tall, erect, some branched at around mid-height, others unbranched, with 6–9 elongated internodes; internodes 3–4.5 cm long, hollow, glabrous, stramineous; prophyll 2.5–4 cm long, strongly 2-keeled, ciliate along the keels, the margins hyaline, glabrous; nodes dark, pilose. Leaves cauline only, symmetrically distributed along the culm or congested at around mid-culm; sheaths round on the back, persistent, striate, glabrous, the margins free, hyaline, both glabrous or one margin ciliate; auricles absent; ligule a minute fringe of hairs, curved, the hairs 0.3–0.5 mm long, colorless, dense; hairs behind the ligular area 2–6 mm long, colorless, sometimes caducous in older leaves; collar undifferentiated, but seen in fresh material as a lighter or purplish area; blades 6–10 cm long and 3–8 mm wide, linear-lanceolate, glabrous on both surfaces but rough on the adaxial surface, the margins glabrous but rough, the apex subpungent to pungent; blades of the lower leaves caducous, the upper blades persistent. Peduncle 2–4.5 cm long, from

partially enclosed in the flag leaf to exserted, glabrous. Inflorescence 6.5–14.5 cm long and 1.5–3.5 cm wide, a contracted, terminal panicle, oblong-lanceolate, pointed at the apex, light-colored, smooth; rachis glabrous, tough; ramification verticillate; nodes pilose, the hairs 1–3 mm long, colorless; branches 4–9 mm long, 2–8 per node, glabrous. Axillary inflorescences absent. Pedicels 1–3 mm long, of unequal length, with a few colorless hairs at the base, the hairs 1–3 mm long, the apex of the pedicels discoid, surrounded by a crown of colorless hairs, the hairs 2–4 mm long. Spikelets paired or solitary, all alike, dorsally compressed, smooth, light-colored, 3–3.2 mm long (exclusive of awn), narrowly oblong-lanceolate in outline, disarticulating below the bracts and falling as a unit, with only one bisexual flower; callus undifferentiated but the hairs at the base of the spikelet 1–1.5 mm long, dense, forming a crown, colorless; spikelet bracts 2 [here interpreted as an upper glume and lower lemma—see discussion]; lower glume absent; upper glume as long as the spikelet, embracing the lower lemma almost entirely, membranous, the margins flat but slightly curved around the lateral nerves of the upper lemma in closed spikelets and fitting into the internervial grooves of the lower lemma, 3- to 5-nerved, the lateral nerves pilose-hispid, the midnerve pilose-hispid toward the apex, projected into a straight or irregularly twisted awn; awn 18–26 mm long, antrorsely barbed, highly hygroscopic; lower palea absent; lower floret reduced to only a lemma; lower lemma 3–3.1 mm long, thin, membranous, 3-nerved, the midnerve prominent, pilose-hispid, the internerves shallowly sulcate, the margins hyaline and sharply folded at the lateral nerves, the apex pointed, ciliate; lower palea absent; lower flower absent; upper floret reduced to only the flower; upper lemma absent; upper palea absent; flower bisexual; lodicules 2, conduplicate; stamens 3, the anthers 1.8–2.1 mm long, purple; ovary 0.5–0.8 mm long, glabrous; stigmas 2, separate, purple. Caryopis 1.8–1.9 mm long, narrowly oblong-lanceolate in outline, dorsally compressed, light brown, with persistent stylar bases, loosely fitting inside the glumes when fully developed; hilum elliptical to oblanceolate, dark brown, ca. ⅕ as long as the caryopsis; embryo ca. ⅓ as long as the caryopsis.

TRANSVERSE SECTION OF LEAF BLADE (FIG. 2)

Leaf outline. Leaf blade expanded, undulating gently on the adaxial surface, the undulations slightly more pronounced in association with first-order vascular bundles resulting in shallow adaxial furrows on either side, without abaxial ribs.

Midrib. Consisting of a single first-order vascular bundle similar in structure to the lateral first-order vascular bundles with no additional associated parenchyma or keel.

Vascular bundle arrangement. 3(or 4) third-order bundles between the first-order bundles; 3 or 4 fourth-order bundles, represented by solitary distinctive Kranz cells between third-order bundles or between first-order and third-order bundles; all bundles more or less centrally located, but first-order and third-order bundles slightly off-center adaxially and fourth-order bundles slightly off-center abaxially.

Vascular bundle description. Third-order bundles vertically elongated and often nearly dumbbell-shaped in outline, with xylem and phloem indistinguishable. First-order bundles vertically elongated in outline. Metaxylem vessels narrow, that is, parenchyma sheath cells wider than the vessel elements; no lysigenous cavity and enlarged protoxylem element present.

Vascular bundle sheaths. In third-order bundles outer parenchyma sheath vertically elongated, complete, composed of 9 to 11 cells, without adaxial or abaxial extensions, with a single large colorless cell located on each side of the sheath in about the center of the blade with the adjoining one or two parenchyma bundle sheaths usually distinctively smaller than the majority of the parenchyma bundle sheath cells.

In first-order bundles outer parenchyma sheath vertically elongated, with or without a slight adaxial interruption and with a wide abaxial interruption, composed of 10 to 13 cells, with a single, large colorless cell similar to those of the third-order bundles on each side of the sheath; parenchyma sheath cells distinct from the chlorenchyma cells with the radial and inner tangential walls straight and the outer tangential walls somewhat rounded, all cells equally thickened.

Sclerenchyma girders. Adaxial sclerenchyma girders associated with first- and second-order bundles, narrowing toward the bundles: girders never associated with fourth-order bundles; abaxial sclerenchyma girders associated with all first- and second-order bundles, well developed, narrowing toward the bundle.

Chlorenchyma. Not distinctly radiate, continuous between the epidermides and between the bundles; without arm cells, fusoid cells, lacunae, or colorless cells.

Adaxial epidermal cells. Groups of bulliform cells present only over groups of fourth-order bun-

dles, not over third- or first-order bundles, fan-shaped, situated at the base of slight furrows, the central cell ca. ⅓ as wide as the leaf thickness, the epidermal cells with the outer tangential walls slightly concave and a thin, continuous cuticle; macrohairs and papillae not present; prickles in both the costal and intercostal zones.

Abaxial epidermal cells. Bulliform cells not present; all cells with a continuous, thick cuticle, ca. twice as thick as the adaxial cuticle. The radial cell walls somewhat thickened; papillae absent; prickles absent.

ADAXIAL EPIDERMIS IN SURFACE VIEW (FIG. 3B)

Intercostal long cells. Elongated 3–5 times longer than wide, rectangular in shape; cell walls moderately thickened; anticlinal cell walls vertical; horizontal anticlinal walls moderately undulate; cell shape relatively constant, cell size variable in single files. Single short cells usually present between 75% or more of successive long cells. Stomata: absent. Papillae: absent. Prickles: numerous in both the intercostal and costal zones. Microhairs: absent. Silica bodies: varying from squarish and angular with irregular outlines to cuboid, more or less squarish with rounded corners.

ABAXIAL EPIDERMIS IN SURFACE VIEW (FIG. 3A, C, D)

Intercostal long cells. Elongated 2.5–3.7 times longer than wide, rectangular in shape, cell walls slightly thickened, anticlinal vertical cell walls angled, horizontal cell walls moderately to slightly undulate; cell shape relatively constant; cell size variable in a single file; pairs or single short cells sometimes present between successive long cells. Stomata: Subsidiary cells low dome-shaped to low-triangular-shaped; four rows of stomata in each intercostal zone most common, usually in double rows adjoining the costal zones; intercostal long cells 1.5–3 times longer than wide, one or two interstomal cells between successive stomata of a row. Single short cells present between costal long cells.

Papillae absent. Prickle hairs present between both costal and intercostal successive long cells. Microhairs infrequent, bicellular, but only the basal cell visible in our preparations [microhairs present on both the upper glume and lower lemma, bicellular, elongated, the basal ca. ½ as long as the distal cell, less than twice as long as wide, with thicker walls than the distal cell, the distal cell more than twice the width, the apex sharply pointed] (Fig. 3C, D).

Silica bodies equidimensional, round to squarish with irregular outlines.

NOTES

The soft texture of the inflorescence and spikelets is intriguing since the caryopsis seems to get almost no protection from the flowering bracts. The most common pattern in the Paniceae in general seems to be that when one bract is missing, the remaining bracts become hardened and protective in function, so as to compensate for the missing structure. *Altoparadisium chapadense* seems to be an outstanding exception to this rule. The bracts here are scarcely hard enough to protect the flower and later the caryopsis. In the later stages of development, the caryopsis remains rather loose inside the bracts. Where does protection for the growing seed and embryo come from? Certainly not from the upper lemma and upper palea, since they are completely lacking. The stiff blades may, to some extent, provide some indirect protection by discouraging the approach of large herbivores, but surely not small herbivores, such as insects, which appear to play an important role in the predation of grass leaves and fruits in the Cerrado vegetation (Filgueiras, 1989).

The generic name alludes to the town of Alto Paraíso in whose municipality the original population was discovered. The specific epithet refers to the Chapada dos Veadeiros, and at the same time honors the Chapadense family of Goiás, Brazil, whose members have been supportive and interested in the work of one us (TSF).

Ecology. Flowering plants in the field have a rather bambusoid appearance, with stiff, congested leaves around mid-culm level. Non-flowering plants have normal-looking blades. The branching of the culms seems to vary within the same clump; some plants in a given clump have branched culms whereas others do not.

The original population discovered was found growing in a campo rupestre habitat, on fine white sand and also on rocks. The soil, very shallow, stony, and dry, was a mixture of gravel and sand. Four groups of plants made up this population, with 2, 5, 15, and 20 clumps respectively. Each of these clumps had from 2 to 12 flowering culms. The groups of plants were situated 50 to 100 m from each other, and the entire population covered an area of approximately 200 m². It is very likely that other populations exist in the area, but none were located, although at that time of the year (September) the light-colored inflorescences of *A. chapa-*

dense stand out against the dry, brown colors of the campo rupestre landscape.

Plants of *A. chapadense* were growing in association with the following species: *Axonopus brasiliensis* (Spreng.) Kuhlm., *Echinolaena inflexa* (Poir.) Chase (the campo rupestre form), *Elionurus muticus* (Spreng.) Kuntze, *Lagenocarpus* sp., *Paspalum polyphyllum* Nees, etc. Except for *E. inflexa*, which flowers almost year-round, no plants of these species were in flower on 5 September 1994. Although the plants were collected during the peak of the flowering period for this population, the leaves had an old, dried out appearance and some had dropped their blades. Almost all the blades displayed some characteristic, irregularly shaped dark spots, suggestive of fungal infection.

During a second trip to the same locality 78 days after the first (24 November 1994), after the first rains had already fallen, it was found that the seeds of *A. chapadense* had long since been dispersed and new growth could be observed at the base of the clumps. At that time, three live plants of *A. chapadense* were taken from the wild and planted at the Reserva Ecológica do IBGE (ca. 15°57'S, 47°52'W), a conservation unit in the Distrito Federal, Brazil, where they are growing well. Two of these plants were planted directly in the ground, and one is being cultivated in a clay pot. In both cases the soil is red latosol, without the use of organic or chemical fertilizers. The plants under cultivation have not developed the above-mentioned dark spots on the blades. Since transplantation, all these plants have flowered four times, always in the last week of August through September. As of September 2000, no seedlings of *A. chapadense* have been observed in the vicinity of the mother clumps under cultivation.

In August 1997 a second population of *A. chapadense* was discovered in the municipality of Niquelândia, state of Goiás, about 145 km west of Alto Paraíso, on the grounds of a private ecological preserve (owned by a local mining firm, "Companhia de Níquel Tocantins") called "Fazenda Engenho." The plants in this population grow in an area ecologically similar to the plants in the Alto Paraíso population. According to the collectors of the plants from the latter population, the plants grew in scattered clumps in an area of approximately 100 m².

Paratype. BRAZIL. **Goiás:** Niquelândia, Fazenda Engenho, Lama Preta, ca. 11 km Niquelândia, 14°39'08"S, 48°26'23"W, 14 Aug. 1997, *F. Oliveira et al. 839* (IBGE, MEXU, VEN).

2. **Altoparadisium scabrum** (Pilg. & Kuhlm.) Filg., Davidse, Zuloaga & Morrone, comb. nov. Basionym: *Arthropogon scaber* Pilg. & Kuhlm., Comm. Lin. Telegr., Bot. 67(anex. 5): 37, pl. 2. 3 Mar. 1922. TYPE: Brazil. Mato Grosso: Cáceres, Agua Quente, *Hoehne 2015* (holotype, R!). See Filgueiras (1982) for further information about the problems with the labeling of the type collection. Figure 7.

Arthropogon scaber Kuhlm. & Pilg., Revista Mus. Paul. Univ. São Paulo 13: 1249. 24 Dec. 1922, nom. illeg. hom. TYPE: Brazil. Mato Grosso: nos campos de Juruena, etc., June 1909, *Hoehne 2016* (holotype, B; isotype, US-865392 (fragm. ex B)!).

2a. **Altoparadisium scabrum** var. **scabrum**

2b. **Altoparadisium scabrum** (Pilg. & Kuhlm.) Filg., Davidse, Zuloaga & Morrone var. **bolivianum** (Filg.) Filg., Davidse, Zuloaga & Morrone, comb. nov. Basionym: *Arthropogon bolivianus* Filg., Brittonia 38: 71. 1986. TYPE: Bolivia. Santa Cruz: near the Arches, 5 km N of Santiago of Chiquitos, 700 m, 2 Sep. 1942, *Cutler 7023* (holotype, US-2013303!).

2c. **Altoparadisium scabrum** (Pilg. & Kuhlm.) Filg., Davidse, Zuloaga & Morrone var. **rupestre** (Filg.) Filg., Davidse, Zuloaga & Morrone, comb. nov. Basionym: *Arthropogon rupestris* Filg., Nordic J. Bot. 16: 69, f. 1. 1996. TYPE: Brazil. Goiás: Serra do Caiapó, 17°12'S, 51°47'W, ca. 50 km S of Caiapônia on road to Jataí, 26 Oct. 1964, *Irwin & Soderstrom 7390* (holotype, SP!; isotype, US!).

Arthropogon Nees, Fl. Bras. Enum. Pl. 2: 319. 1829. TYPE: *Arthropogon villosus* Nees.

KEY TO THE SPECIES OF *ARTHROPOGON*

1a. Upper glume with the apex entire; leaf blades cylindrical .... *A. filifolius*
1b. Upper glume with the apex bilobed; leaf blades flat.
   2a. Lower lemma awned, the apex bilobed ......
   .... *A. xerachne*
   2b. Lower lemma muticous, the apex entire ....
   .... *A. villosus*

1. **Arthropogon filifolius** Filg., Bradea 3(21): 151, f. 1. 1981. TYPE: Brazil. Distrito Federal: Cabeça do Veado, capim de espiguetas aristadas, crescendo em brejo recém queimado, 15 Sep. 1980, *T. S. Filgueiras 671* (holotype, IBGE!; isotypes, R!, RB!, SP!, US-2946634!).

Known only from Brazil (Goiás, Minas Gerais, and the Distrito Federal).

Additional specimen examined. BRAZIL. **Minas Gerais:** Uberlândia, just N of town, left side RR, 850–870 m, 15 Mar. 1930, *Chase 11261 1/2* (US).
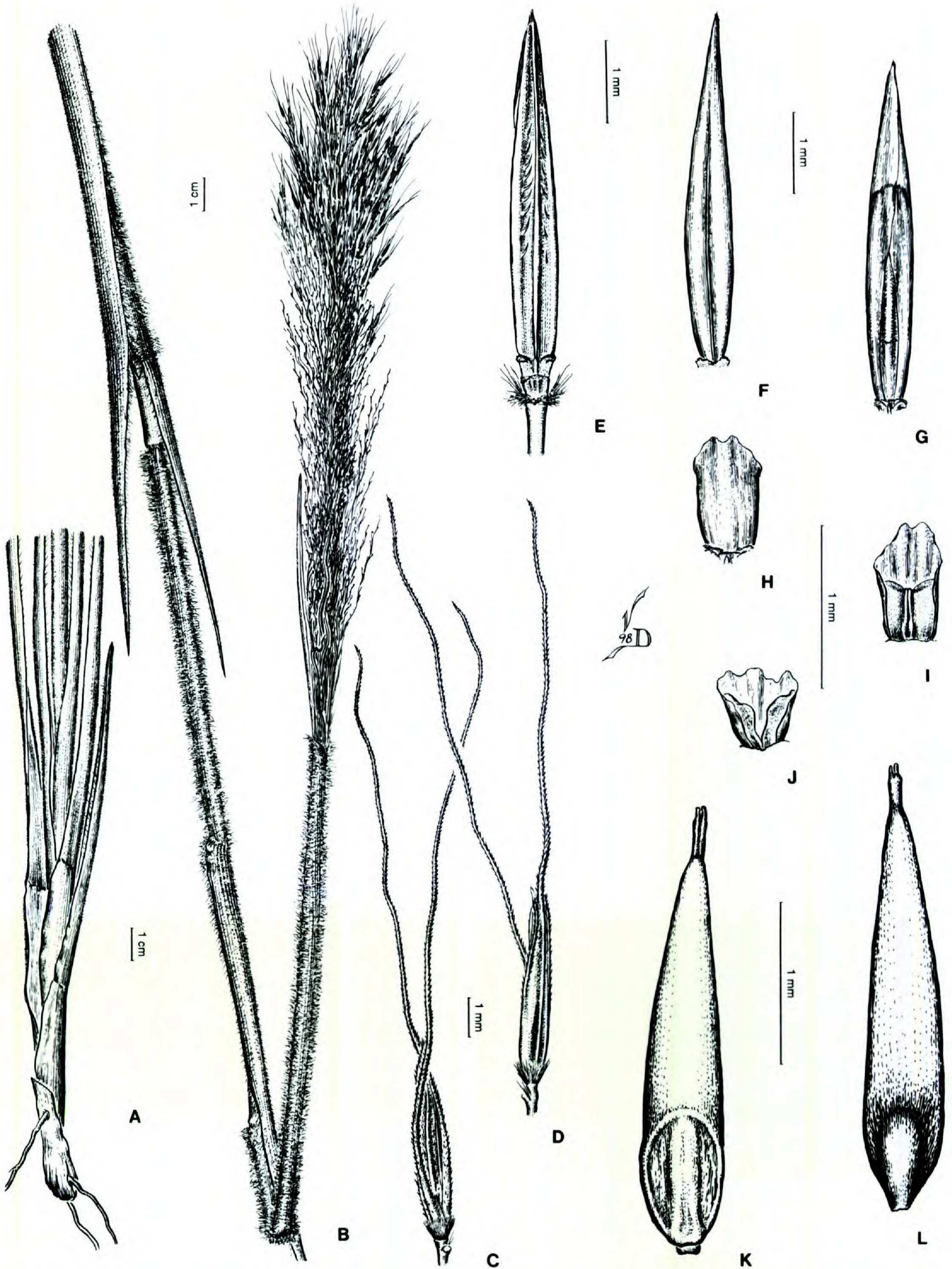
Figure 7. *Altoparadisium scabrum* var. *scabrum* (based on *Kuhlmann 1853*, US). —A. Base of the plant. —B. Habit, upper portion of a culm with a terminal inflorescence. —C. Spikelet seen from the side of the lower glume with hairs at the apex of the pedicel and the base of the callus. —D. Spikelet seen from the side of the upper glume. —E. Lower floret seen from the side of the lower lemma, with prominent nerves, and base of the spikelet with callus. —F. Upper lemma, dorsal view. —G. Upper lemma, ventral view, with stamens and reduced palea at the base. —H. Upper palea, dorsal view. —I. Upper palea and lodicules, ventral view. —J. Upper palea, ventral view. —K. Caryopsis, embryo side. —L. Caryopsis, hilum side. All drawings by Vladimiro Dudás.

2. **Arthropogon villosus** Nees, Fl. Bras. Enum.
Pl. 2: 320. 1829. TYPE: Brazil. "Habitat in
campis altis Chapada of Paranan provinciae
Minarum versus Goyaz, et ad Rio Fermoso,"
Martius s.n. (holotype, M!; isotype fragment,
US-865393!).

Known from Brazil (Bahia, Distrito Federal,
Goiás, Mato Grosso, Minas Gerais, Paraná, and São
Paulo), and Bolivia (Santa Cruz).

Additional specimens examined. BRAZIL. **Bahia:** 22
km S of the Rio Galheirao along Hwy. BR-020, 860 m, 8
Apr. 1976, *Davidse et al. 12222* (US), *12222A* (MO). **Dis-
trito Federal:** burned-over campo and cerrado, summit
of Chapada da Contagem, ca. 10 km NE of Brasília, 1000
m, 11 Sep. 1965, *Irwin et al. 8174* (MO); cerrado, gallery
forest and adjacent burned-over cerrado, Córrego Urubu,
wet slopes of Chapada da Contagem, ca. 10 km E of Bra-
sília, 1000 m, 14 Sep. 1965, *Irwin et al. 8309* (MO); cer-
rado ca. 20 km S of Brasília on road to Goiânia, near Rio
Melchoir, 1125 m, 25 Sep. 1965, *Irwin et al. 8661* (MO).
Mato Grosso: Braco, Rio Arinos, 26 Sep. 1943, *Baldwin
3041* (US). **Minas Gerais:** Lavras, 4 Mar. 1925, *Chase
8844* (MO); Serra do Cipó, Km 106-90 (110 km NE of
Belo Horizonte), 800 m, 28 Mar.–1 Apr. 1925, *Chase 9283*
(MO); S. Vicente, 10 Nov. 1956, *Macedo 2711* (MO, US).
Goiás: Uruaçu, Fazenda Macaco, margem esquerda do
córrego vermelho, 6 Oct. 1992, *Pinheiro C. et al. II 0041*
(MO); hwy. between Planaltina and São Gabriel de Goiás
ca. 5 km S of São Gabriel, 29 Nov. 1988, *Kral et al. 75720*
(MO). **Paraná:** ad Morungava praedium pr. Itararé op-
positum in campo, 720 m, 7 Dec. 1915, *Dusén 17406*
(MO). BOLIVIA. **Santa Cruz:** Ñuflo de Chavez, Concep-
ción, 500 m, 7 Aug. 1985, *Killeen 1112* (MO); Ñuflo de
Chavez, Est. San Josecito, 2 km NE of Concepción, 500
m, 7 Sep. 1985, *Killeen 1178* (MO).

3. **Arthropogon xerachne** Ekman, Ark. Bot.
10(17): 9, pl. 1, f. 4, pl. 6, f. 4. 1911. TYPE:
Brazil. São Paulo: S. José dos Campos, in cam-
po, 1910, *Löfgren 243* (lectotype, here desig-
nated, S!; isolectotype, US-3168439 frag-
ment!). This specimen is chosen as the
lectotype because it agrees perfectly with the
description, and because it has the most de-
tailed locality data.

Known from Brazil (Paraná and São Paulo).

Additional specimens examined. BRAZIL. **Paraná:**
without locality, 23 June 1910, *Dusén 10002* ([syntypes]S,
US-3168438 fragment); Jaguariahyva, in campo cerrado,
730 m, 30 Nov. 1915, *Dusén 17367* (SI), 22 Oct. 1910,
Dusén 10748 (MO). **São Paulo:** Mun. S. José dos Cam-
pos, 6.8–7.2 km ao SSE em linha reta da praça principal
of São José dos Campos, 12 Sep. 1962, *Mimura 563* (US);
Campinas, 12 Dec. 1940, *Viegas & Lima s.n.* (US-
1764757).

Achlaena Griseb., Cat. Pl. Cub. 228. 1886. TYPE:
Achlaena piptostachya Griseb.

1. **Achlaena piptostachya** Griseb., Cat. Pl.
Cuba: 229. 1866. *Arthropogon piptostachyus*
(Griseb.) Pilg., Revista Mus. Paul. Univ. São
Paulo 13: 1250. 1922. *Arthropogon piptostach-
yus* (Griseb.) Tateoka, Bot. Mag. (Tokyo)
76(902): 290. 1963, isonym. TYPE: Cuba.
Without locality, *Wright 3487* (holotype?; iso-
types, NY!, US-927103!, US-75310 frag-
ment!).

Known from Cuba and Jamaica.

Additional specimens examined. CUBA. Río Piloto, Si-
erra de Nipe, Oriente, savannas on eruptive rock, 8 Sep.
1922, *Ekman Amer. Gr. Nat. Herb. 800* (MO). JAMAICA.
Hanover: Ashkenish to Dophin Head, pasture on clay
soil, 8 Sep. 1960, *Adams 7952* (MO).

Literature Cited

Bentham, G. & J. D. Hooker. 1883. Gramineae. *In* Gen-
era Plantarum 3(2): 1074–1215. L. Reeve, London.
Bews, J. W. 1929. The World's Grasses. Longmans,
Green, London.
Blake, S. T. 1958. New criteria for distinguishing genera
allied to *Panicum* (Gramineae). Proc. Roy. Soc. Queens-
land 70: 15–19.
Bremer, K. 1994. Branch support and tree stability. Cla-
distics 10: 295–304.
Brown, W. V. 1977. The Kranz syndrome and its subtypes
in grass systematics. Mem. Torrey Bot. Club 23: 1–97.
Burkart, A. 1969. Gramíneas. Fl. Il. Entre Ríos. Colecc.
Ci. Inst. Nac. Tecnol. Agropecu. 6(2): 1–551.
Butzin, F. 1972. Zur Nomenklatur und Taxonomie der
Arthropogoneae (Gramineae, Panicoideae). Willdenowia
6: 511–517.
Chase, A. 1911. Notes on genera of Paniceae. IV. Proc.
Biol. Soc. Wash. 24: 103–160.
Cialdella, A. M. & A. S. Vega. 1996. Estudios sobre la
variación estructural de las espiguillas en genéros de la
tribu Paniceae (Poaceae). Darwiniana 34: 173–182.
Clayton, W. D. & S. A. Renvoize. 1986. Genera gramin-
um. Grasses of the world. Kew Bull., Addit. Ser. 13: 1–
389.
Cochrane, T. T., S. Nichez, L. G. Azevedo, J. A. Porras &
C. L. Garver. 1985. Land in Tropical America. Cali,
CIAT- MBRAPA-CPAC.
Cutler, D. 1978. Applied Plant Anatomy. Academic
Press, London.
Dengler, N. G., R. E. Dengler & P. W. Hattersley. 1985.
Differing ontogenetic origins of PCR ("Kranz") sheaths
in leaf blades of C_4 grasses (Poaceae). Amer. J. Bot. 72:
284–302.
Ekman, E. L. 1911. Neue brasilianischer Gräser. Ark.
Bot. 10(17): 1–15.
Ellis, R. P. 1976. A procedure for standardizing compar-
ative leaf blade anatomy in the Poaceae. I. The leaf
blade as viewed in transverse section. Bothalia 12: 65–
109.
———. 1977. Distribution of the Kranz syndrome in the
Southern African Eragrostideae and Panicoideae ac-

cording to bundle sheath anatomy and cytology. Agro-plantae 9: 73–110.

———. 1979. A procedure for standardizing comparative leaf blade anatomy in the Poaceae. II. The epidermis as seen in surface view. Bothalia 12: 641–672.

———. 1987. A review of comparative leaf blade anatomy in the systematics of the Poaceae: The past twenty-five years. Pp. 3–10 in T. R. Soderstrom, K. W. Hilu, C. S. Campbell & M. E. Barkworth (editors), Grass Systematics and Evolution. Smithsonian Institution Press, Washington, D.C.

———. 1988. Leaf anatomy and systematics of Panicum (Poaceae: Panicoideae) in southern Africa. Monogr. Syst. Bot. Missouri Bot. Gard. 25: 129–156.

Farris. J. S. 1988. Hennig86. Reference, version 1.5. Port Jefferson Station. J. S. Farris, New York.

———. 1989. The retention index and the rescaled consistency index. Cladistics 5: 417–419.

Felfili, J. A., T. S. Filgueiras, M. Haridasan, M. C. Silva Jr., R. C. Mendonça & A. V. Rezende. 1994. Projeto biogeografia do bioma Cerrado: vegetação e solos. Cadernos de Geociências, 12: 75–166.

———, M. C. Silva Jr., A. V. Rezende, P. E. Nogueira, B. M. T. Walter & M. A. Silva. 1997. Composição florística e fitossociológica do cerrado na Chapada dos Veadeiros. Pp. 6–11 in L. Leite & C. H. Sato (editors), Contribuição ao Conhecimento Ecológico do Cerrado. Brasília, Editora da Universidade de Brasília.

Felsenstein, J. 1985. Confidence limits on phylogenetics: An approach using the bootstrap. Evolution 39: 783–791.

Filgueiras, T. S. 1981. Species duae graminearum Brasiliae novae. Bradea 3: 151–155.

———. 1982. Taxonomia e distribuição de Arthropogon Nees (Gramineae). Bradea 3: 303–322.

———. 1986. A new species of Arthropogon (Gramineae: Arthropogoneae) and a revised key for the genus. Brittonia 38: 71–72.

———. 1989. Gramíneas e herbívoros considerações sobre o processo de coevolução adaptativa. Ciência e Cultura 41: 158–162.

———. 1996. Arthropogon rupestris (Poaceae: Arthopogoneae) a new species from the Brazilian cerrado vegetation and a revised key for the genus. Nordic J. Bot. 16: 69–72.

——— & F. O. Zuloaga. 1999. A new Triraphis (Poaceae: Eragrostideae) from Brazil: First record of a native species in the New World. Novon 9: 36–42.

Goloboff, P. A. 1993. NONA versión 1.8 (32 bit). Programa y documentación distribuida por el autor. Tucumán, Argentina.

Grisebach, A. 1866. Catalogus Plantarum Cubensium. Leipzig.

Hackel, E. 1887. Gramineae. In A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien 2(2): 1–97. Engelmann, Leipzig.

Hattersley, P. W. & L. Watson. 1975. Anatomical parameters for predicting photosynthetic pathways of grass leaves: The "maximum lateral cell count" and the "maximum cells distant count." Phytomorphology 25: 325–333.

——— & ———. 1976. C$_4$ grasses: An anatomical criterion for distinguishing between NADP-Malic enzyme species and PCK or NAD-Malic enzyme species. Austral. J. Bot. 24: 297–308.

——— & ———. 1992. Diversification of photosynthesis. Pp. 38–116 in G. P. Chapman (editor), Grass Evo-lution and Domestication. Cambridge Univ. Press, Cambridge.

Hitchcock, A. S. 1936. Manual of the Grasses of the West Indies. United States Department of Agriculture Miscellaneous Publication 243: 1–439.

Hoehne, F. C. & R. Pilger. 1922. Novidades da flora mattogrossense e do Hervario da Comissão Rondon. Revista Mus. Paul. Univ. São Paulo 13: 1247–1254.

Hsu, C. C. 1965. The classification of Panicum (Gramineae) and its allies, with special reference to the characters of lodicule, style-base and lemma. J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 9: 43–150.

Hubbard, C. E. 1929. Notes on African grasses, VIII. Snowdenia, a new genus from Uganda. Bull. Misc. Inform. Kew 1929: 28–31.

Jacques-Félix, H. 1962. Les Graminées (Poaceae) d'Afrique Tropicale, I: Généralités classification, description des genres. Institut des Recherches Agronomiques Tropicales et des Cultures Vivrières, Bulletin Scientifique (Paris) 8: i–xi, 1–345.

Judziewicz, E. 1990. Family 187. Poaceae. In A. R. A. Görts-van Rijn (editor), Flora of the Guianas. Series A: Phanerogams. Koeltz Scientific Publications, Koenigstein, Germany.

Kellogg, E. A. & C. S. Campbell. 1987. Phylogenetic analyses of the Gramineae. Pp. 310–322 in T. R. Soderstrom, K. W. Hilu, C. S. Campbell & M. E. Barkworth (editors), Grass Systematics and Evolution. Smithsonian Institution Press, Washington, D.C.

——— & L. Watson. 1993. Phylogenetic studies of a large data set. I. Bambusoideae, Andropogonodae, and Pooideae (Gramineae). Bot. Rev. 59: 273–340.

Killeen, T. & L. G. Clark. 1986. Fusoid-like cells in Panicum section Laxa (Poaceae: Panicoideae). Amer. J. Bot. 73: 771.

Kluge, A. G. & J. S. Farris. 1969. Quantitative phyletics and evolution of anurans. Syst. Zool. 18: 1–32.

Kuhlmann, J. G. 1922. Gramineas. Comm. Lin. Telegr., Bot. 67(Bot. 11): 1–95, t. 1–6.

Kunth, C. S. 1833. Enumeratio Plantarum . . . Agrostographia Synoptica . . . Supplement to Vol. 1. J. G. Cottae. Stuttgart, Tübingen.

Metcalfe, C. R. 1960. Anatomy of the Monocotyledons, Vol. 1: Gramineae. Clarendon Press, Oxford.

Morrone, O. & F. O. Zuloaga. 1991. Revisión del género Streptostachys (Poaceae–Panicoideae), su posición sistemática dentro de la tribu Paniceae. Ann. Missouri Bot. Gard. 78: 359–376.

———, ——— & E. Carbonó. 1995. Revisión del grupo Racemosa del género Paspalum (Poaceae: Panicoideae: Paniceae). Ann. Missouri Bot. Gard. 82: 82–116.

Munhoz, C. B. R. & C. E. B. Proença. 1998. Composição florística do município de Alto Paraíso na Chapada dos Veadeiros. Bol. Herb. Ezechias Paulo Heringer 3: 102–150.

Nees von Esenbeck, C. G. D. 1829. Flora Brasiliensis seu Enumeratio . . . , C. F. D. von Martius (editor), 2(1): 1–608.

Nicora, E. G. & E. Rúgolo de Agrasar. 1987. Los Géneros de Gramíneas de América Austral. Hemisferio Sur, Buenos Aires.

Nixon, K. C. 1993. Clados, version 1.38 [32 bit] beta version. Computer program distributed by the author.

Pilger, R. 1954. Das System der Gramineae. Bot. Jahrb. Syst. 76: 281–384.

Reger, B. J. & I. E. Yates. 1979. Distribution of photosynthetic enzymes between mesophyll specialized

chlorenchyma and bundle sheath cells of *Arundinella hirta*. Pl. Physiol. 63: 209–212.

Renvoize, S. A. 1982a. A survey of leaf blade anatomy in grasses II. Arundinelleae. Kew Bull. 37: 489–495.

———. 1982b. A survey of leaf blade anatomy in grasses III. Garnotieae. Kew Bull. 37: 497–500.

———. 1987. A survey of leaf blade anatomy in grasses XI. Paniceae. Kew Bull. 42: 739–768.

———. 1998. Gramíneas de Bolivia. Continental Printing, Belgica.

Rosengurtt, B., B. R. Arrillaga de Maffei & P. Izaguirre de Artucio. 1970. Gramíneas Uruguayas. Publicaciones de la Universidad de la República, Montevideo.

Roshevits, R. Y. 1937. Zlaki. Vvedeniye v isucheniye kormovykh i khlebnykh zlakov [Grasses. An Introduction to the Study of Fodder and Cereal Grasses]. Moscow, Leningrad.

Sánchez, E. & M. Arriaga. 1989. El síndrome de Kranz en Arundinelleae (Panicoideae–Poaceae) de la flora sudamericana. Parodiana 5: 261–277.

———, M. O. Arriaga & R. P. Ellis. 1989. Kranz distinctive cells in the culm of *Arundinella* (Arundinelleae; Panicoideae; Poaceae). Bothalia 19: 45–52.

Sendulsky, T., T. S. Filgueiras & A. G. Burman. 1987. Fruits, embryos and seedlings. Pp. 31–36 in T. R. Soderstrom, K. W. Hilu, C. S. Campbell & M. E. Barkworth (editors), Grass Systematics and Evolution. Smithsonian Institution Press, Washington, D.C.

Smith, B. N. & W. V. Brown. 1973. The Kranz syndrome in the Gramineae as indicated by carbon isotopic ratios. Amer. J. Bot. 60: 505–513.

Soderstrom, T. R. & R. P. Ellis. 1987. The position of bamboo genera and allies in a system of grass classification. Pp. 225–238 in T. R. Soderstrom, K. W. Hilu, C. S. Campbell & M. E. Barkworth (editors), Grass Systematics and Evolution. Smithsonian Institution Press. Washington, D.C.

Steudel, E. G. 1853–1855. Synopsis Plantarum Glumacearum, Part 1. Synopsis Plantarum Graminearum. J. B. Metzler, Stuttgart.

Tateoka, T. 1958. Notes on some grasses, VIII. On leaf structure of *Arundinella* and *Garnotia*. Bot. Gaz. (Tokyo) 120: 101–109.

———. 1963. Notes on some grasses XV. Affinities and species relationship of *Arthropogon* and relatives, with reference to their leaf-structure. Bot. Mag. (Tokyo) 76: 286–291.

Watson, L. & M. J. Dallwitz. 1992. The Grass Genera of the World. C. A. B. International, Wallingford.

——— & M. J. Dallwitz. 1992 onward. Grass Genera of the World: Descriptions, Illustrations, Identification, and Information Retrieval; Including Synonyms, Morphology, Anatomy, Physiology, Phytochemistry, Cytology, Classification, Pathogens, World and Local Distribution, and References. Version: 28th May 1999. http://biodiversity.uno.edu/delta/

———, H. T. Clifford & M. J. Dallwitz. 1985. The classification of Poaceae: Subfamilies and supertribes. Austral. J. Bot. 33: 433–484.

Webster, R. D. 1988. Genera of the North American Paniceae (Poaceae: Panicoideae). Syst. Bot. 13: 576–609.

———. 1992. Character significance and generic similarities in the Paniceae (Poaceae: Panicoideae). Sida 15: 185–213.

———, J. H. Kirkbride & J. Valdés Reyna. 1989. New World genera of the Paniceae (Poaceae: Panicoideae). Sida 13: 393–417.

Wills, K. E., R. D. B. Whalley & J. J. Bruhl. 2000. Systematics studies in Paniceae (Poaceae): *Homopholis* and *Whalleya*, gen. et sp. nov. Austral. Syst. Bot. 13: 437–468.

Zuloaga, F. O. & T. R. Soderstrom. 1985. Classification of the outlying species of New World *Panicum* (Poaceae: Paniceae). Smithsonian Contr. Bot. 59: 1–63.

———, R. P. Ellis & O. Morrone. 1992. A revision of *Panicum* subgenus *Phanopyrum* section *Laxa* (Poaceae: Panicoideae: Paniceae). Ann. Missouri Bot. Gard. 79: 770–818.

———, O. Morrone & L. Giussani. 2000. A cladistic analysis of the Paniceae: A preliminary approach. Pp. 123–135 in S. W. L. Jacobs & J. Everett (editors), Grasses: Systematics and Evolution. CSIRO, Melbourne.

APPENDIX 1.

MORPHOLOGICAL CHARACTERS

Inflorescence: character 1

Inflorescence morphology is variable in the positioning of the primary branches. In this study we designate as compact those inflorescences in which the primary branches form an angle of less than 30° from the main rachis; and as open those inflorescences with the primary branches more than 30° (usually 45°).

Pilose callus: character 2; *stipe*: character 4; and *base torose*: character 33

The presence of a differentiated structure at the base of spikelet has been termed a callus or stipe (Burkart, 1969; Rosengurtt et al., 1970; Nicora & Rúgolo de Agrasar, 1987; Judziewicz, 1990; Watson & Dallwitz, 1992; Renvoize, 1998). Webster (1992) mentioned the presence of a callus in 21 genera of Paniceae, but did not distinguish whether the structures were homologous. Since such general designations may involve very different structures or a combination of different structures, they must be more precisely defined in order to estimate homology.

In this study we define a pilose callus to be a whorl of unicellular macrohairs at the base of the spikelet that is clearly differentiated from the rest of the surface. A stipe is defined as a sharply pointed structure derived from the fusion of the base of the lower glume with the enlarged rachilla internode between the lower and upper glume. This occurs in *Arthropogon piptostachyus*. A toroid base is defined as an enlarged ringlike growth formed from the lateral enlargement of the rachilla of the internode between the lower glume and the upper floret. In *Streptostachys* this structure functions as an elaiosome at spikelet maturity (Morrone & Zuloaga, 1991).

Spikelet compression: character 3

The compression of the spikelets is a diagnostic character for distinguishing genera of the Paniceae (Clayton & Renvoize, 1986; Webster, 1988). Lateral compression is recognized by the form of the bracts, which are usually keeled and folded along the length of the midnerve. Dorsal compression is recognized by the form of the bracts, which are rounded or flattened dorsally and with the plane of compression opposite to the plane formed by the midnerve of the spikelet bracts.

Spikelet bracts: characters 5, 6, 7, 8, 9, 10, 13, 14, 15, 22, 26, 28, 29, 31, and 34

Genera of Paniceae usually possess two-flowered spikelets with two glumes, one lower lemma and palea forming the lower floret and one upper lemma and palea forming the upper floret. However, variations of this basic organizational plan occur in many of the genera in our study. *Thyridolepis, Homolepis, Streptostachys, Digitaria, Homo-*

pholis, Melinis, Achlaena, and *Arthropogon* s.l. all possess the lower and upper glume, the lower lemma, and the upper lemma and palea. The lower palea is present in *Homolepis, Anthaenantia, Arthropogon villosus, A. filifolius, A. xerachne,* and *A. lanceolatus,* but is variously reduced in *Thyridolepis, Streptostachys, Digitaria, Melinis,* and *Arthropogon bolivianus.*

Another reduction series affects the lower glume. The presence or absence of the lower glume is an important character for recognizing genera in the Panicoideae (Webster, 1988; Judziewicz, 1990; Renvoize, 1998). Clayton and Renvoize (1986) and Watson and Dallwitz (1992) treated *Anthaenantia* and *Leptocoryphium* as related to each other and characterized both by the absence of a lower glume. A third reduction series occurs in *Reynaudia* in which both the lower and upper palea are absent.

Texture of lower glume: character 34

The texture of the lower glume in the Paniceae varies from herbaceous, hyaline, transparent, or rigidly setaceous and awnlike.

Texture of upper glume and lower lemma: characters 28 and 29

The texture of the upper glume and lower lemma in Paniceae is variable; it may be coriaceous or membranous. The apex of the upper glume and lower lemma is entire or bilobed; the midnerve may be prolonged into a slender awn. When developed, the awn may be straight or twisted and in the latter case is then hygroscopic. The nerves of the upper glume and lower lemma may be delicate or enlarged, in the last case with deep intercostal grooves.

Upper floret: characters 12, 16, and 26

The most diagnostic characters in the Paniceae involve the upper lemma and upper palea, which together form the upper floret (Chase, 1911; Webster, 1988). Similar to the spikelets as a whole, the upper floret may be laterally or dorsally compressed. Lemma texture is an important character in the delimitation of genera of Paniceae (Chase, 1911; Blake, 1958; Hsu, 1965; Clayton & Renvoize, 1986). The lemma of the taxa in this study may be coriaceous or hyaline, and its color varies from straw-colored to castaneous or translucent. Since the texture and color vary with the development of the spikelets, care was taken to only use only mature spikelets, and when possible, one enclosing a mature caryopsis. In the absence of a hypothesis about the evolution of the color of the upper floret, this character was treated as an unordered one.

Hilum: character 25

Hilum types in the Paniceae vary considerably, but there are no general studies dealing with evolution of this character in this tribe. In the Paniceae the punctate type of hilum is most frequent, followed by the linear type. Zuloaga and Soderstrom (1985), Filgueiras (1986), Sendulsky et al. (1987), and Morrone and Zuloaga (1991) considered the hilum type to be a useful taxonomic character. For this study, the hilum was considered to be linear when it occupies the entire length of the caryopsis and punctate when it is no longer than ¼ as long as the caryopsis.

Germination lid: character 27

The presence of a well-defined germination lid is variable in the Paniceae. Blake (1958) indicated that its presence constituted a significant character in the Paniceae, but it has been underutilized.

ANATOMICAL CHARACTERS (CHARACTERS 18–21, 23, 30)

Characters 19 and 20 deal with the photosynthetic pathway and with the Kranz syndrome. Brown (1977) and Ellis (1977, 1988) established the importance of anatomical leaf characters for analyzing relationships within the Paniceae. These authors demonstrated the presence of diverse anatomical and physiological types in the tribe, including C_3 and C_4 types in the plants under investigation, with the latter further subdivided as subtypes nicotinamide adenine dinucleotide co-factor malic enzyme (NAD-me), phosphoenol pyruvate carboxykinase (PCK), k and nicotinamide adenine dinucleotide phosphate co-factor malic enzyme (NADP-me). In order to establish the homologies of the different structures involved in each anatomical type, we follow the criteria proposed by Brown (1977) and Dengler et al. (1985). They considered that the Kranz sheath of the NADP-me anatomical type is homologous to the mestome (= MS) sheath of C_3 plants, and that the Kranz sheath of the NAD-me or PEP-ck is homologous to the parenchyma (= PS) sheath of C_3 grasses.

The distinctive Kranz cells (character 20) are distributed in the mesophyll and are not associated directly with vascular tissue. As Tateoka (1958) had done earlier, Hattersley and Watson (1992) interpreted distinctive Kranz cells to be vestiges or extreme reductions of the sheaths of minor vascular bundles. However, the absence of associated vascular tissue with the distinctive Kranz cells and the lack of ontogenetic studies to interpret homology in relation to meristematic origin caused us to treat this character separately.

The presence of fusoid cells (character 21) is diagnostic for the Bambusoideae (Metcalfe, 1960; Jacques-Félix, 1962; Soderstrom & Ellis, 1987; Ellis, 1987), but they also occur in *Homolepis* (Watson et al., 1985; Renvoize, 1987; Watson & Dallwitz, 1992), *Streptostachys* (Clayton & Renvoize, 1986; Renvoize, 1987), and in species of *Panicum* sect. *Laxa* (Killeen & Clark, 1986; Zuloaga et al., 1992). In these panicoid taxa the fusoid cells are globose, transversally enlarged, with thin cell walls and without intercellular spaces evident in transverse sections, whereas intercellular spaces occur in the Bambusoideae.

APPENDIX 2. LIST OF SPECIMENS EXAMINED FOR THE CLADISTIC ANALYSIS

Achlaena piptostachya Griseb.

CUBA: Without locality, *Wright 3487* (isotypes, US-927103, fragment, US-75310); hills SE of Soledad, 30 Nov. 1926, *Hitchcock 23333* (US). **Isla de la Juventud:** San Pedro region, white-sand sabanas, 18 Mar. 1954, *Killip 43960* (US); near Nueva Gerona, 17 Dec. 1903, *Curtiss 2?6* (US). **Pinar del Río:** along camino Aguacate from Bahía Honda to Baños Aguacate, 11 Dec. 1910, *Wilson 9?15* (US); Taco-Taco, Sierra de los Organos, 400–500 m, 1? Nov. 1941, *Morton 4365* (US).

Altoparadisium chapadense Filg. et al.

BRAZIL. **Goiás:** Chapada dos Veadeiros, município de Alto Paraíso, ca. 26 km a Oeste of Alto Paraíso, ca. 14°0?'S–47°30'W, campo rupestre, estrada para Colinas do Sul Goiás, 5 Sep. 1994, *T. S. Filgueiras & M. L. Fonseca 2?87* (isotype, SI).

Altoparadisium scabrum (Pilg. & Kuhlm.) Filg. et al. var. ***scabrum***

BRAZIL. **Mato Grosso:** Cáceres, Agua Quente, *Kuhlmann 1853* (isotype, US-A0865392).

Altoparadisium scabrum (Pilg. & Kuhlm.) Filg. et al. var. ***bolivianum*** (Filg.) Filg. et al.

BOLIVIA. **Santa Cruz:** near the Arches, 5 km N of Santiago of Chiquitos, 700 m, 2 Sep. 1942, *Cutler 7023* (holotype, US-2013303).

Altoparadisium scabrum (Pilg. & Kuhlm.) Filg. et al.
var. *rupestre* (Filg.) Filg. et al.

BRAZIL. **Goiás:** Serra do Caiapó, 17°12'S, 51°47'W, ca. 50 km S of Caiapônia on road to Jataí, 26 Oct. 1964, *Irwin & Soderstrom 7390* (fragment of isotype, US).

Anthaenantia rufa (Elliot) Schult.

U.S.A. **Texas:** 5 mi. NW of Groveton, *Gould 12001* (SI).

Anthaenantia villosa (Michx.) P. Beauv.

U.S.A. **Florida:** ca. 15 mi. N of Pensacola, *Silveus 5622* (US).

Arthropogon filifolius Filg.

BRAZIL. **Distrito Federal:** Cabeça do Veado, Capim de espiguetas aristadas, crescendo em brejo recém queimado, 15 Sep. 1980, *T. S. Filgueiras 671* (US-2946634). **Minas Gerais:** Uberlandia, just N of town, left side RR, 850–870 m, 15 Mar. 1930, *Chase 11261 1/2* (US).

Arthropogon lanceolatus Filg.

BRAZIL. **Minas Gerais:** Furnas, Ribeirão das Pacas-Cascatas, 28 July 1966, *Emygdio 2308* (isotype, US-2979541).

Arthropogon villosus Nees

BRAZIL. "Habitat in campis altis Chapada of Paranan provinciae Minarum versus Goyaz, et ad Rio Fermoso," *Martius s.n.* (isotype fragment, US-865393). **Bahia:** 22 km S of the Rio Galheirao along Hwy. BR-020, 860 m, 8 Apr. 1976, *Davidse et al. 12222* (US). **Mato Grosso:** Braco, Rio Arinos, 26 Sep. 1943, *Baldwin 3041* (US). **Minas Gerais:** Carmo, 26 Sep. 1948, *Macedo 1246* (US); S. Vicente, 10 Nov. 1956, *Macedo 2711* (US). **São Paulo:** Serra da Cunha, 1200 m, 14 Mar. 1939, *Kuhlman & Gehrt s.n.* (US-2917179); Mun. S. José dos Campos, 6.8–7.2 km ao SSE em linha reta de praça principal de São José dos Campos, 12 Sep. 1962, *Mimura 557* (US).

Arthropogon xerachne Ekman

BRAZIL. **São Paulo:** S. José dos Campos, in campo, 1910, *Löfgren 243* (syntype, US-3168439, fragment); Mun. S. José dos Campos, 6.8–7.2 km ao SSE em linha reta da praça principal of São José dos Campos, 12 Sep. 1962, *Mimura 563* (US); Campinas, 12 Dec. 1940, *Viegas & Lima s.n.* (US-1764757). **Paraná:** without locality, 23 June 1910, *Dusén 10002* (syntype, US-3168438, fragment); Jaguariahyva, in campo cerrado, 730 m, 30 Nov. 1915, *Dusén 17367* (SI), 22 Oct. 1911, *Dusén 13231* (SI, US); São José dos Campos, Sep. 1908, *Löfgren 3820* (US); Mun. S. José dos Campos, 7.5 km S of São José dos Campos, along highway to Paraibuna, 31 May 1961, *Eiten & Sendulsky 2867* (US).

Digitaria ciliaris (Retz.) Koel.

ARGENTINA. **Santiago del Estero:** Sierra de Guasayán, Quebrada de Conzo, 16 Feb. 1989, *Ulibarri 1566* (SI).

Digitaria sanguinalis (L.) Scop.

U.S.A. **Florida:** Altamonte Spring, 25 Apr. 1959, *Schallert 10441* (SI).

Digitaria setigera Roth

COLOMBIA. **Antioquia:** Mun. Andes, 12.5 km de los Andes hacia el Corregimiento de Tapartó, 24 Aug. 1988, *Fonnegra et al. 2476* (SI).

Homolepis aturensis (Kunth) Chase

BOLIVIA. **Beni:** Guayamerim, *Krapovickas & Schinini 35109* (CTES). BRAZIL. **Amazonas:** Barcelãos Negro river, *Baldwin 3330* (US). **Pernambuco:** Recife, *Pickel 3608* (US). COLOMBIA. **Cauca:** Chisquío, Finca de Derrumbes, *Asplund 10558* (US).

Homopholis belsonii C. E. Hubb.

AUSTRALIA. Jondaryan, Darling Downs District, 1250 ft., 12 Feb. 1938, *Blake 13252* (MO).

Leptocoryphium lanatum (Kunth) Nees

ARGENTINA. **Corrientes:** Dpto. Capital, 15 km al S de la ciudad de Corrientes, Riachuelo, 16 Dec. 1983, *Hunziker et al. 11091* (SI). **Entre Ríos:** Depto. Colón, Palmar, a 13 km E de Ruta Nac. 14, camino al Palmar, 17 Jan. 1976, *Romanczuk et al. 56* (SI). **Misiones:** Dpto. San Ignacio, San Ignacio, 11 Oct. 1975, *Zuloaga & Deginani 450* (SI). BOLIVIA. **Santa Cruz:** Buena Vista, 30 Sep. 1916, *Steinbach 2882* (SI). PARAGUAY. **Itapúa:** Isla Yaciretá, camino al aeródromo de Yaciretá, 27°22'S, 56°38'W, 23 Apr. 1992, *Morrone & Pensiero 237* (SI).

Melinis minutiflora P. Beauv.

BRAZIL. **Bahia:** Mun. de Ilhéus, estrada Olivenca-Maruim, entre los kms 7–10, restinga arbórea, 19 May 1985, *Zuloaga et al. 2478* (SI). **Paraná:** Porto Amazonas, ad ripam fluminis Rio Iguassú, 800 m, 10 June 1914, *Dusén 15154* (SI). **Santa Catarina:** Sombrio, 50 m, 29 May 1945, *Reitz 1130* (SI). **Pernambuco:** Tapera, Sep. 1930, *Pickel 97* (SI). PERU. **Cajamarca:** Prov. Cutervo, a 22 km sobre la carretera Cutervo–Sócota, 2450 m, 15 June 1980, *Sánchez Vega 2296* (SI). VENEZUELA. **Miranda:** Los Teques, faldas de cerros, 14 Mar. 1946, *Burkart 16012* (SI).

Reynaudia filiformis (Spreng. ex Schult.) Kunth

DOMINICAN REPUBLIC. Llano Costero, Higüey, savanna 2 km W of town, 17 Apr. 1929, *Ekman 12208* (MO).

Streptostachys asperifolia Desv.

BRAZIL. **Amapá:** Porto Platón, *Mattos 10120* (SP, US). **Goiás:** 2 km N of Araguainia, *Irwin et al. 21133* (F, NY, US). **Pará:** near Soure, Marajó Island, *Goeldi 299* (US). VENEZUELA. **Sucre:** 7 km E of the Mochima Hwy., intersection along Hwy. 9 between Cumaná and Puerto la Cruz, *Davidse 5044* (MO).

Thyridolepis multiculmis (Pilg.) S. T. Blake

AUSTRALIA. **Northern Territory:** Uluru National Park, on the Docker River road near the W park boundary, 55 km WNW of the Ranger Station, 25°17'S, 130°40'W, 18 Aug. 1988, *Lazarides & Palmer 535* (MO).